

IMPERIAL AGRICULTURAL
RESEARCH INSTITUTE, NEW DELHI.

LIST OF CONTENTS.

1930, pp. 549–1080.

EXHIBITIONS AND NOTICES.

Page

The Secretary. Note on two Lion-Tiger Hybrids 845

Miss E. M. Brown, B.Sc. Exhibition of Protozoan Parasites of Fishes..... 845

Mr. E. G. Boulenger, F.Z.S. Exhibition of living specimens of the Poison-Frog (*Dendrobates tinctorius*) and Midwife-Toad (*Alytes obstetricans*) 845

The Secretary. Report on the Additions to the Society's Menagerie during the month of April, 1930 845

Major S. S. Flower, O.B.E., F.Z.S. Exhibition of photographs of animals in the Carl Hagenbeck Tierpark 846

Mr. D. Seth-Smith, F.Z.S. Exhibition of photographs of the first Pigmy Hippopotamus (*Chæropsis liberiensis*) born in the Society's Gardens ... 846

Col. A. E. Hamerton, C.M.G., D.S.O., F.Z.S. Exhibition of photographs and remarks on "Trypanosomiasis in relation to Man and Beast in Africa" 846

Mr. J. R. Norman, F.Z.S. Exhibition of Pectoral Fin of the Flying-Fish (*Exocœtus fernandezianus*) 847

Col. S. Monckton Copeman, M.D., F.R.S., F.Z.S. Exhibition of specimen and photograph of a rare variety in the Waved Umber Moth (*Hemerophila abruptaria* var. *unicolor*) 847

The Secretary. Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1930 1077

Dr. W. T. Calman, F.R.S., F.Z.S. Exhibition of photograph of a living *Anaspides tasmaniæ*. (Text-figure 1.) 1079

Prof. T. Thomson Flynn, D.Sc. Exhibition of embryonic material from the Echidna (*Tachyglossus*) 1079

Page

Mr. W. B. Cotton, I.C.S., F.Z.S. Exhibition of Ears and Molars of an African Elephant 1079

The Secretary. Exhibition of photographs of African Elephants taken by Mr. M. A. Wetherall 1080

Mr. J. R. Norman, F.Z.S. Exhibition of photographs of a living Shark with a Remora attached 1080

Mr. E. G. Boulenger, F.Z.S. Exhibition of (1) a red variety of the Common Lobster, and (2) eggs of a Sea-Snake (*Laticauda colubrina*) ... 1080

The Secretary. Report on the Additions to the Society's Menagerie during the month of October, 1930 1080

The Secretary. Exhibition of photograph of House-Sparrow (*Passer domesticus* Linn.) with abnormal growth of beak 1080

Prof. R. T. Leiper, D.Sc., M.D., F.R.S., F.Z.S. Exhibition of Helminth infection in Brain of Man 1080

Dr. F. A. Bather, F.R.S., F.Z.S. Remarks on the Resolutions on Zoological Nomenclature passed at the Zoological Congress, Padua, 1930 1080

PAPERS.

29. A Classification of the Original Watercolour Paintings of the Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London. By G. Carmichael Low, M.A., M.D., F.R.C.P., F.Z.S., Douglas Dewar, B.A., F.Z.S., T. H. Newman, F.Z.S., and G. A. Levett-Yeats, C.I.E., I.S.O., V.D., F.Z.S. (Map.). 549

30. The Bionomics and Morphology of the Early Stages of *Paraphœdon tumidulus* Germ. (Coleoptera, Phytophaga, Chrysomelidæ).—Part I. By Nellie F. Paterson, M.Sc., Ph.D. (Plates I.–IV.; Text-figures 1–17.) 627

31. On a New Dipterous Parasite (Family Calliphoridæ, Subfamily Calliphorinæ) of the Indian Elephant, with Notes on other Dipterous Parasites of Elephants. By Major E. E. Austen, D.S.O., F.Z.S. (Text-figures 1–3.) 677

32. Indian Mantids or Praying Insects. By F. Werner, C.M.Z.S. (Plate I.) 689

Page

33. The Menstrual Cycle of the Primates.—Part 1. General Nature and Homology. By S. ZUCKERMAN, M.A., M.R.C.S., L.R.C.P. (Plates I. & II.; Charts 1–14; Diagrams 1–4.) 691

34. The Development of the Heart in the Rabbit. By A. GIRGIS, M.Sc., M.R.C.S. (Plates I.-XI.; Text-figures 1–4.) 755

35. Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*. By AGNES E. MILLER, M.A. (Plate I.; Text-figures 1–5.) 783

36. Notes on the Habits and Feeding Mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida). By S. M. MANTON, M.A., Ph.D., F.L.S. (Plates I.–IV.; Text-figure 1.)... 791

37. Animal Life in the Marsh Ditches of the Thames Estuary. By F. J. LAMBERT. (Map.) 801

38. The Ecology of the American Grey Squirrel (*Sciurus carolinensis* Gmelin) in the British Isles. By A. D. MIDDLETON. (Plates I.–VI.; Text-figures 1–4.) 809

39. The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio. By MARGARET C. STEEN, B.Sc. (Plates I.–VI.; Text-figure 1–21.) 849

40. On the Budding of a Scyphistoma. By RACHEL M. RENTON, F.Z.S. (Plate I.; Text-figure 1.) 893

41. A Collection of Frogs from Portuguese East Africa. By H. W. PARKER, B.A. (Plate I.; Text-figure 1.)..... 897

42. The Attachments of the Urodele Rib to the Vertebra, and their Homologies with the Capitulum and Tuberculum of the Amniote Rib. By PETER GRAY, B.Sc., A.R.C.S. (Plate I.; Text-figures 1 & 2.)..... 907

43. Report on the Hydracarina. Mr. Omer-Cooper's Investigation of the Abyssinian Fresh Waters (Dr. Hugh Scott's Expedition). By Dr. C. WALTER. (Text-figures 1–18.) 913

44. The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* (Diptera, Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini). By W. H. THORPE, M.A., Ph.D., C.M.Z.S. (Plates I.–V.; Text-figures 1–23.) 929

45. On Entomostraca from the New Hebrides collected by Dr. J. R. Baker. By A. G. LOWNDES, M.A., C.M.Z.S. (Plates I. & II.)..... 973

46. Notes on Stegocephalia and Amphibia. By Dr. FRANCIS, Baron NOPCSA, C.M.Z.S., For. Memb. Geol. Soc..... 979

Page

47. The Proportions of Birds' Wings and their changes during Development. By B. J. Marples, B.A., the Victoria University of Manchester. (Text-figures 1–7.) 997

48. The Structure and Life-history of *Sciara nitidicollis* Meig. (Diptera). By Iuan Thomas, M.Sc. (Wales). (Text-figures 1–14.) 1009

49. The Natural History and Variation of the Pointed Snail, *Cochlicella acuta* (Müll.). By D. Aubertin, M.Sc., A. E. Ellis, B.A., and G. C. Robson, M.A., F.Z.S. (Plate I.; Text-figures 1 & 2, and Tables I.–III.) 1027

50. Testudinate Evolution. By P. E. P. Deraniyagala, M.A. Cantab., A.M. Harvard. (Plates I.–III.) 1057

51. The Otoliths of some Large Eels from the Lake of Tunis. By Dr. A. Gandolfi Hornyold, F.R.M.S., F.Z.S. (Plates I.–IV.) 1071

Alphabetical List of Contributors vii

Index of Illustrations xi

Index xiii

ALPHABETICAL LIST.

OF THE

CONTRIBUTORS.

With References to the several Articles contributed by each.

(1930, pp. 549–1080.)

Page

AUBERTIN, D., M.Sc., ELLIS, A. E., B.A., and ROBSON, G. C., M.A., F.Z.S.

The Natural History and Variation of the Pointed Snail, *Cochlicella acuta*. (Plate I.; Text-figures 1 & 2, and Tables I.–III.) 1027

AUSTEN, Major E. E., D.S.O., F.Z.S.

On a New Dipterous Parasite (Family Calliphoridæ, Subfamily Calliphorinæ) of the Indian Elephant, with Notes on other Dipterous Parasites of Elephants. (Text-figures 1–3.) 677

BATHER, Dr. F. A., F.R.S., F.Z.S.

Remarks on the Resolutions on Zoological Nomenclature passed at the Zoological Congress, Padua, 1930 1080

BOULENGER, E. G., F.Z.S. (Director of the Aquarium).

Exhibition of living specimens of the Poison-Frog (*Dendrobates tinctorius*) and Midwife Toad (*Alytes obstetricans*) 845

Exhibition of a red variety of the Common Lobster, and eggs of Sea-Snake (*Laticauda colubrina*) 1080

BROWN, Miss E. M., B.Sc. (Aquarium Research Fellow).

Exhibition of Protozoan Parasites of Fishes.. 845

CALMAN, Dr. W. T.. F.R.S., F.Z.S.

Exhibition of photograph of a living *Anaspides tasmaniæ*. (Text-figure 1.) 1078

COPEMAN, Col. S. MONCKTON, M.D., F.R.S., F.Z.S.

Exhibition of specimen and photograph of a rare variety of the Waved Umber Moth (*Hemerophila abruptaria* var. *unicolor*) 847

Page

COTTON, W. B., I.C.S., F.Z.S.
Exhibition of Ears and Molars of an African Elephant 1079

DERANIYAGALA, P. E. P., M.A., A.M. Harvard.
Testudinate Evolution. (Plates I.–III.)..... 1057

DEWAR, DOUGLAS. *See* LOW, G. CARMICHAEL.

ELLIS, A. E. *See* AUBERTIN, D.

FLOWER, Major S. S., O.B.E., F.Z.S.
Exhibition of photographs of animals in the Carl Hagenbeck Tierpark ... 846

FLYNN, Prof. T. THOMSON, D.Sc.
Exhibition of embryonic material from the Echnida (*Tachyglossus*)..... 1079

GIRGIS, A., M.Sc., M.R.C.S.
The Development of the Heart in the Rabbit. (Plates I.–XI.; Text-figures 1–4.)..... 755

GRAY, PETER, B.Sc., A.R.C.S.
The Attachments of the Urodele Rib to the Vertebra, and their Homologies with the Capitulum and Tuberculum of the Amniote Rib. (Plate I.; Text-figures 1 & 2.) 907

HAMERTON, Col. A. E., C.M.G., D.S.O., F.Z.S. (Pathologist to the Society.)
Exhibition of photographs and remarks upon "Trypanosomiasis in relation to Man and Beast in Africa" 846

HORNYOLD, Dr. GANDOLFI, F.R.M.S., F.Z.S.
The Otoliths of some large Eels from the Lake of Tunis. (Plates I.-IV.). 1071

LAMBERT, F. J.
Animal Life in the Marsh Ditches of the Thames Estuary. (Map.) ... 801

LEIPER, Prof. R. T., D.Sc., M.D., F.R.S., F.Z.S.
Exhibition of Helminth infection in Brain of Man..... 1080

LEVETT-YEATS, G. A. *See* LOW, G. CARMICHAEL.

LOW, G. CARMICHAEL, M.A., M.D., F.R.C.P., F.Z.S., DEWAR, DOUGLAS, B.A., F.Z.S., NEWMANN, T. H., F.Z.S., and LEVETT-YEATS, G. A., C.I.E., I.S.O., V.D., F.Z.S.
A Classification of the Original Watercolour Paintings of the Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London. (Map.)..... 549

Page

LOWNDES, A. G., M.A., C.M.Z.S.

On Entomostraca from the New Hebrides collected by Dr. J. A. Baker. (Plates I. & II.) 973

MANTON, S. M., M.A., Ph.D., F.L.S.

Notes on the Habits and Feeding Mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida). (Plates I.–IV.; Text-figure 1.) ... 791

MARPLES, B. J., B.A.

The Proportions of Birds' Wings and their Changes during Development. (Text-figures 1–7.) 997

MITCHELL, Sir PETER CHALMERS, C.B.E., M.A., D.Sc., LL.D., F.R.S. (Secretary to the Society).

Note on two Lion-Tiger Hybrids 845

Report on the Additions to the Society's Menagerie during the month of April, 1930 845

Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1930 1077

Exhibition of photographs of African Elephants 1080

Report on the Additions to the Society's Menagerie during the month of October, 1930 1080

Exhibition of photograph of House-Sparrow with abnormal growth of beak 1080

MIDDLETON, A. D.

The Ecology of the American Grey Squirrel (*Sciurus carolinensis* Gmelin) in the British Isles. (Plates I.–VI.; Text-figures 1–4.) 809

MILLER, AGNES E., M.A.

Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*. (Plate I.; Text-figures 1–5.) 783

NEWMAN, T. H. *See* LOW, G. CARMICHAEL.

NOPCSA, FRANCIS, Baron, C.M.Z.S.

Notes on Stegocephalia and Amphibia 979

NORMAN, J. R., F.Z.S.

Exhibition of Pectoral Fin of the Flying-Fish (*Exocœtus fernandezianus*). 847

Exhibition of photograph of a living Shark with a Remora attached ... 1080

Page

PARKER, H. W., B.A.

A Collection of Frogs from Portuguese East Africa. (Plate I.; Text-figure 1.) 897

PATERSON, NELLIE F., M.Sc., Ph.D.

The Bionomics and Morphology of the Early Stages of *Paraphædon tumidulus* Germ. (Coleoptera, Phytophaga, Chrysomelidæ). (Plates I.–IV.; Text-figures 1–17.) 627

RENTON, RACHEL M., F.Z.S.

On the Budding of a Scyphistoma. (Plate I.; Text-figure 1.)..... 893

ROBSON, G. C. *See* AUBERTIN, D.

SETH-SMITH, D., F.Z.S. (Curator of Birds and Mammals).

Exhibition of photographs of the first Pigmy Hippopotamus (*Chæropsis liberiensis*) born in the Society's Gardens 846

STEEN, MARGARET C., B.Sc.

The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio. (Plates I.–VI.; Text-figures 1–21.)..... 849

THOMAS, IEUAN, M.Sc.

The Structure and Life-History of *Sciara nitidicollis* Meig. (Text-figures 1–14.) 1009

THORPE, W. H., M.A., Ph.D., C.M.Z.S.

The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* (Diptera, Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini). (Plates I.–V.; Text-figures 1–23.) ... 929

WALTER, Dr. C.

Report on the Hydracarina. Mr. Omer-Cooper's Investigation of the Abyssinian Fresh Waters (Dr. Hugh Scott's Expedition). (Text-figures 1–18.) 913

WERNER, F., C.M.Z.S.

Indian Mantids or Praying Insects. (Plate I.) 689

ZUCKERMAN, S., M.A., M R.C.S., L.R.C.P. (Anatomist to the Society).

The Menstrual Cycle of the Primates.—Part I. General Nature and Homology. (Plates I. & II.; Charts 1–14; Diagrams 1–4.) 691

ZOOLOGICAL SOCIETY OF LONDON.

INSTRUCTIONS TO AUTHORS.

Owing to the cost of printing, the Publication Committee beg to draw the attention of Authors submitting papers for publication by the Society to the following Regulations. If the conditions are not observed, papers may have to be returned :—

1. MSS. submitted for publication must be written in a clear and legible handwriting, or, preferably, be type-written, and must be in final form for printing. The MSS. should be written on one side of each sheet only, and the pages clearly numbered. All tables of contents, references to plates, or legends to illustrations in the text, etc., must be in their proper places, **with page and plate numbers left blank**; and the position for the text-figures must be indicated. References to literature must be exact, with the page number as well as the volume number and date.

Contributors of papers involving extensive numerical observations are requested to consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from the British Association, Burlington House, W. 1, price 6*d*.

Arrangements have been made whereby original data, too extensive for complete publication, may be deposited at the British Museum (Natural History) or with the Royal Society of Edinburgh, and so be made available for future workers. Authors desirous of depositing data, whether zoological or botanical, in this manner should communicate with either the Keeper of Zoology, Natural History Museum, S.W. 7, or the General Secretary, The Royal Society of Edinburgh, 22 George Street, Edinburgh, enclosing full bibliographic reference to the publication in which the results are summarised.

2. Proofs and their Correction.—Two copies of the slip proof, and a page proof for final revision, will be sent to the Author, **but it is important that all serious corrections be made on the slip proof.** Expenses for proof corrections are very heavy, but, if the MSS. comply with Regulation 1, should not exceed 25 per cent. of the printers' charges. If the cost of corrections exceeds 25 per cent., a proportion of the excess will be charged to the Author.

3. Revised proofs must, if possible, be returned within one week from the date of their receipt by the Author.

4. The Author receives 30 copies of reprints free, and, with the sanction of the Publication Committee, may obtain leave to buy extra copies, at the cost price charged by the printers and engravers to the Society. The number of separate copies required must be stated when returning the proof.

5. ILLUSTRATIONS.—Drawings intended to be reproduced as line-block text-figures should be drawn with a good black ink, such as "Process Black" or the best "Indian ink" on white "Bristol board." All lines and dots must be clear and sharp, and no washes or colours used. Wash drawings are not suitable for reproduction as text-figures. All necessary lettering **must be clearly, but lightly, indicated in pencil**, so that the engravers may insert sharp, well-drawn letters. Each drawing should be numbered to tally with the text-figure number given in the MSS., and be accompanied by a short, concise, and legible descriptive legend. When making drawings for text-figures, or grouping drawings, it should be borne in mind that, when reduced, the figures must not exceed the dimensions of the printed matter on the page of "Proceedings," viz.:—$4\frac{1}{2} \times 6\frac{1}{2}$ inches. Drawings or photographs intended for reproduction as plates will have to be reduced, when necessary, to fit a space of $5 \times 7\frac{1}{2}$ inches.

6. COPYRIGHT.—No use whatever is permitted of the type or illustrations prepared for the Society's Publications other than for the Separate Copies mentioned above, unless the leave of the Committee has been obtained, and recorded on the Minutes. Permission is given only with the consent of the Authors of the papers, if alive, and the source of the text and illustrations shall be stated in the work in which they are used. The use of illustrations from the Society's Publications, if within five years of the date of publication, will be granted only upon the payment of half the cost of their production. All communications made to the Society shall, if accepted for publication, be regarded as the property of the Society, and not returned to the Authors, except for the purpose of comparison with the proof when set up in type.

Note.—The Publication Committee is always ready to give Authors who apply for it, permission to reproduce matter that they have contributed to the Society's "Proceedings" and "Transactions," but the Society has been advised that a formal assignment from Authors is necessary to enable it to protect copyright against third parties.

ZOOLOGICAL SOCIETY OF LONDON.

THIS Society was founded in 1826 by Sir STAMFORD RAFFLES, Sir HUMPHRY DAVY, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

Patron.

HIS MAJESTY THE KING.

COUNCIL.

HIS GRACE THE DUKE OF BEDFORD, K.G., F.R.S., *President.*

FIELD-MARSHAL THE VISCOUNT ALLENBY, G.C.B., G.C.M.G., *Vice-President.*

RICHARD H. BURNE, ESQ., M.A., F.R.S.

COL. S. MONCKTON COPEMAN, M.D., F.R.S.

CHARLES DRUMMOND, ESQ., *Treasurer.*

ALFRED EZRA, ESQ., O.B.E.

MAJOR STANLEY S. FLOWER, O.B.E., F.L.S.

HUGH S. GLADSTONE, ESQ., M.A., F.R.S.E.

THE RT. HON. THE VISCOUNT GREY OF FALLODON, K.G., P.C., F.R.S., *Vice-President.*

LT.-COL. THE RT.-HON. WALTER E. GUINNESS, P.C. D.S.O., M.P.

PROF. JAMES P. HILL, D.SC., F.R.S.

LT.-COL. THE LORD ALASTAIR INNES-KER, D.S.O.

PROF. ERNEST W. MACBRIDE, M.A., F.R.S., *Vice-President.*

SIR P. CHALMERS MITCHELL, C.B.E., M.A., D.SC., LL.D., F.R.S., *Secretary.*

THE EARL OF ONSLOW, P.C., O.B.E. *Vice-President.*

MAJOR ALBERT PAM, O.B.E.

LT.-COL. SIR DAVID PRAIN, C.M.G., C.I.E., F.R.S.

C. TATE REGAN, ESQ., M.A., D.SC., F.R.S.

THE LORD ROTHSCHILD, D.SC., F.R.S. *Vice-President.*

ANTHONY H. WINGFIELD, ESQ., D.L.

SIR ARTHUR SMITH WOODWARD, LL.D., F.R.S., *Vice-President.*

The Society consists of Fellows, Imperial Fellows, Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.R.M.S., F.R.P.S., F.Z.S., is open daily (except Sunday) from Ten A.M. till Five P.M.; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning during the month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Vevers is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Mr. L. C. Bushby, F.E.S., is Curator of Insects; Mr. S. Zuckerman, M.A., M.R.C.S., L.R.C.P., is Anatomist; Col. A. E. Hamerton, C.M.G., D.S.O., Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

TERMS FOR THE ADMISSION OF FELLOWS.

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can be deemed a FELLOW until the Admission Fee and first Annua Subscription of £3 have been paid, or the annual payments have been compounded for.

The usual Admission Fee of £5 is waived upon the election of the WIFE or HUSBAND of an existing FELLOW.

The First Annual Subscription of Fellows elected in November and December covers the following year.

PRIVILEGES OF FELLOWS.

Fellows have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The Wife or Husband of a Fellow can exercise these privileges in the absence of the Fellow, but this privilege cannot be extended to children of Fellows.

Until further notice, Fellows, unless they have exercised the option stated in the next sentence receive each year 40 undated Green cards, available on any Sunday or week-day up to the end of January of the year following the year of issue, and 20 White cards available on any week-day up to the same date. For 20 Green tickets, however, they may receive a book of dated Sunday orders, each admitting two persons, but valid only for the actual days printed on them, and in exchange for twenty White tickets, a similar book of week-day orders, each valid only for the week printed on it. Special children's tickets are no longer issued, as the Green and White cards are perforated, and each half is valid for a Child under twelve years of age. Additional Sunday tickets cannot be purchased or acquired. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not available.

Fellows are not allowed to pass in friends on their written order or on presentation of their visiting cards.

Aquarium.—Fellows have free personal admission to the Aquarium at all times when it is open. On Sundays, but not on week-days, they may introduce two visitors with them. These privileges are personal and cannot be transferred. The undated Green cards will give admission to the Aquarium to Visitors already in the Gardens, but two tickets will be needed for admission to Gardens and Aquarium. At the same time Fellows are reminded that whereas Aquarium tickets may be purchased it is not possible to obtain additional Sunday tickets giving Admission to the Gardens. For admission to the Aquarium of other friends whom they have admitted to the Gardens by Sunday tickets they may purchase from the Office books of 20 tickets for £1, or a smaller number at the same rate, each ticket admitting one adult or two children on Sundays or week-days. Fellows may also purchase a transferable Aquarium Ivory Ticket, for £10, valid for the whole duration of the Fellowship and admitting daily, on Sundays or week-days, two persons who have already gained admission to the Gardens.

Fellows have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. Fellows are likewise entitled to purchase these Publications at 16⅔ (2*d.* in 1/-) per cent. less than the price charged to the public. A further reduction of 25 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

Fellows also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

FELLOWS may obtain a TRANSFERABLE IVORY TICKET admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any FELLOW who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upn the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any FELLOW, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

P. CHALMERS MITCHELL,
Secretary.

Regent's Park, London, N.W. 8.
January, 1931.

MEETINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

FOR

SCIENTIFIC BUSINESS.

1931.

TUESDAY, FEBRUARY	3 and	17.
——— MARCH	3 ,,	17.
——— APRIL	14 ,,	28.
——— MAY	12 ,,	26.
——— JUNE	9	—

The Chair will be taken at half-past Five o'clock precisely.

ZOOLOGICAL SOCIETY OF LONDON.

LIST OF PUBLICATIONS.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in royal octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An "Abstract of the Proceedings" is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the "Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The "Transactions" contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 16⅔ per cent. (2*d.* in 1/-) less than the price charged to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

4to. 20 vols. and Index.

				Price to Fellows.	Price to the Public.
Vols. I.–IV. (out of print).					
Vol. V., containing	67	Plates ..	(1862–66)	5 15 10	6 19 0
„ VI., „	92	„ ..	(1866–69)	12 10 0	15 0 0
„ VII., „	73	„ ..	(1869–72)	11 6 8	13 12 0
„ VIII., „	82	„ ..	(1872–74) ...	10 9 2	12 11 0
„ IX., „	99	„ ..	(1875–77) ...	13 8 4	16 2 0
„ X., „	95	„ ..	(1877–79) ...	11 2 6	13 7 0
Index, Vols. I.–X.			(1833–79)	0 8 4	0 10 0
Vol. XI., containing	97	Plates ..	(1880–85) ...	10 13 4	12 16 0
„ XII., „	65	„ ..	(1886–90)	6 0 0	7 4 0
„ XIII., „	62	„ ..	(1891–95)	7 2 6	8 11 0
„ XIV., „	47	„ ..	(1896–98)	5 16 8	7 0 0
„ XV., „	52	„ ..	(1898–1901) ..	6 8 4	7 14 0
„ XVI., „	38	„ ..	(1901–1903) ..	6 0 0	7 4 0
„ XVII., „	41	„ ..	(1903–1906) ..	6 11 8	7 18 0
„ XVIII., „	43	„ ..	(1907–1911) ..	4 10 0	5 8 0
„ XIX., „	24	„ ..	(1909–1910) ..	11 6 8	13 12 0
„ XX., „	53	„ ..	(1912–1915) ..	12 15 10	15 7 0
„ XXI.—Part I. (7 Plates & 12 Text-figures.)					
			(June 1916)	2 10 0	3 0 0
„ „ „ II. (5 Plates & 30 Text-figures.)					
			(January 1930)	2 10 0	3 0 0
Vol. XXII., containing 1 Plate & 233 Text-figures.					
			(1926–1929)	12 10 0	15 0 0

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is now able to offer for sale at the reduced price of £30, sets of Vols. V.–XVI. inclusive.

PROCEEDINGS OF THE COMMITTEE OF SCIENCE AND CORRESPONDENCE OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo. 2 vols. (Letterpress only).

			Price to Fellows.	Price to the Public.
Part I.	1830–31.	1 vol. 8vo., out of print.		
„ II.	1832.	„	5*s.* 0*d.*	6*s.*

PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON.

First Series.

Parts I.–XV. (1833–1847). 8vo. 15 vols. (Letterpress only.) Price to Fellows: 5*s.* 0*d.* each part; to the Public, 6*s.*

Index 1830–1847. Price to Fellows: 5*s.* 0*d.*; to the Public, 6*s.*

Parts I., VII.–IX., XI., XIV., XV., out of print.

Second Series.

Parts XVI.–XXVIII. (1848–1860). 8vo. 13 vols. (Letterpress only.) Price to Fellows: 5*s.* 0*d.* each part; to the Public, 6*s.*

Index 1848–1860. Price to Fellows: 5*s.* 0*d.*; to the Public, 6*s.*

The Parts of this series containing Coloured Plates are out of print.

PROCEEDINGS OF THE SCIENTIFIC MEETINGS OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo.

	Letterpress only.		With Plates uncoloured.		With Plates coloured.	
	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public.
1861	5*s.*	6*s.*	10*s.*	12*s.*	37*s.* 6*d.*	45*s.*†
1862	5*s.*	6*s.*	10*s.*	12*s.*	37*s.* 6*d.*	45*s.*†
1863	5*s.*	6*s.*	10*s.*	12*s.*	37*s.* 6*d.*	45*s.*†
1864	5*s.*	6*s.**	10*s.*	12*s.*†	37*s.* 6*d.*	45*s.**
1865	5*s.*	6*s.*†	10*s.*	12*s.*	37*s.* 6*d.*	45*s.*
1866	5*s.*	6*s.*†	10*s.*	12*s.*†	37*s.* 6*d.*	45*s*
1867			10*s.*	12*s.**	37*s.* 6*d.*	45*s*
1868			10*s.*	12*s.*	37*s.* 6*d.*	45*s.*
1869			10*s.*	12*s.*	37*s.* 6*d.*	45*s.*
1870			10*s.*	12*s.*	37*s.* 6*d.*	45*s.*
Index, 1861–1870			5*s.*	6*s.*		
1871			10*s.*	12*s.**	37*s.* 6*d.*	45*s.*†
1872			10*s.*	12*s.**	37*s.* 6*d.*	45*s.*†
1873			10*s.*	12*s.*	37*s.* 6*d.*	45*s.*†
1874			10*s.*	12*s.*†	40*s.*	48*s.*†
1875			10*s.*	12*s.*	40*s.*	48*s.*
1876			10*s.*	12*s.*	40*s.*	48*s.*†
1877			10*s.*	12*s.*	40*s.*	48*s.*
1878			10*s.*	12*s.*	40*s.*	48*s.*
1879			10*s.*	12*s.*	40*s.*	48*s.*
1880			10*s.*	12*s.*	40*s.*	48*s.*
Index, 1871–1880			5*s.*	6*s.*		
1881–1890. Ten volumes			Each		40*s.*	48*s*
Index, 1881–1890			5*s.*	6*s.*		
1891–1900. Ten volumes			Each		40*s.*	48*s.*
Index, 1891–1900			5*s.*	6*s.*		

* No perfect copies in stock.

† Out of print.

PROCEEDINGS OF THE GENERAL MEETINGS FOR SCIENTIFIC BUSINESS OF THE ZOOLOGICAL SOCIETY OF LONDON

(*continued*).

		Price to Fellows.	Price to the Public.
1901–1910.*	Twenty volumes Each	20*s.*	24*s.*
Index, 1901–1910		5*s.*	6*s.*
Index, 1911–1920		8*s.* 4*d.*....	10*s.*
1911–1916.†	Twelve volumes	20*s.*	24*s.*
1917.	Vol. I.	20*s.*	24*s.*
„	„ II.	10*s.*	12*s.*
1918.	Two volumes	10*s.*	12*s.*
1919.	Two volumes	16*s.* 8*d.*....	20*s.*
1920.	Vol. I.	16*s.* 8*d.*....	20*s.*
„	„ II.	20*s.*	24*s.*
1921–1929.	Nine volumes	40*s.*	48*s.*
1930.	Vol. I.	20*s.*	24*s.*
„	„ II.	20*s.*	24*s.*

Commencing with part I. 1929, the size of the Society's "Proceedings" has been increased to Royal Octavo.

* 1908 out of print. 1911 out of print.

† 1925, Vol. I. out of print.

CENTENARY HISTORY of the Society, written by the Secretary. Published price 25*s.* Price to Fellows 20*s.*

LIST OF THE ANIMALS. 1826–1927. Vol. I. Mammals. By Major STANLEY S. FLOWER, O.B.E., F.Z.S. Published price 25*s.* Price to Fellows 20*s.* Vol. II. Birds, by Dr. CARMICHAEL LOW, and Vol. III. Reptiles, Amphibia, and Pisces, by S. S. FLOWER, M. A. SMITH, and E. G. BOULENGER, will be published shortly, price 25*s.* each, to Fellows 20*s.*

THE OFFICIAL ILLUSTRATED GARDEN GUIDE—27th Edition (Revised)—with (1) a Railway and Street Map; (2) a Plan of the Grounds; (3) a short description of some of the principal animals in the Collection, with 55 Photographic Illustrations and Index. Price 1*s.* in Stiff Paper Cover, postage 2*d.*

ILLUSTRATED GUIDE TO THE AQUARIUM. Price 6*d.*, postage 2*d.*

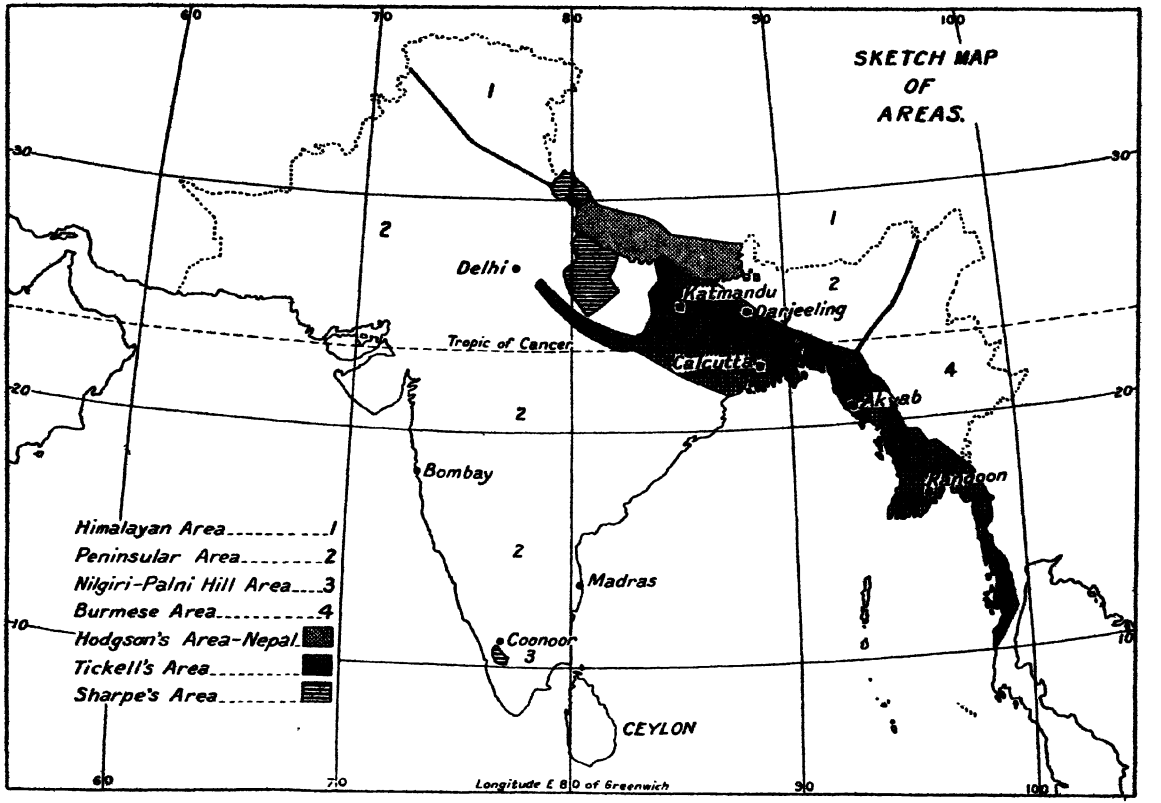
ZOOLOGICAL RECORD.—Vol. 66, containing literature relating chiefly to the year 1929, will shortly be published, price £3. Vol. 67, for the year 1930, is being prepared as usual, price £3, or subscription, if paid in advance, £2 10*s.* 0*d.*

A CLASSIFICATION OF THE ORIGINAL WATERCOLOUR PAINTINGS OF BIRDS OF INDIA by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London. By G. C. Low, DOUGLAS DEWAR, T. H. NEWMAN, and G. A. LEVETT-YEATS. 7*s.* 6*d.*

P. CHALMERS MITCHELL,
Secretary,

Regent's Park, London, N.W. 8.
January, 1931.

These publications may be obtained at the SOCIETY'S OFFICE *or through any bookseller.*



Map showing areas in which Hodgson, Tickell, and Sharpe worked.

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

29. A Classification of the Original Watercolour Paintings of Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London. By G. Carmichael Low, M.A., M.D., F.R.C.P., F.Z.S., Douglas Dewar, B.A., F.Z.S., T. H. Newman, F.Z.S., and G. A. Levett-Yeats, C.I.E., I.S.O., V.D., F.Z.S.

[Received April 16, 1930: Read June 3, 1930.]

(Plate I.)

Foreword.

It has long been felt that the classification of Hodgson's and Tickell's Paintings of the Birds of India in the Zoological Society's Library would be useful, and when a further series of paintings by General C. F. Sharpe was lately acquired, Sir Peter Chalmers Mitchell asked Carmichael Low if he would undertake this work. He said, if some other Fellows of the Society would help, he would do so, and Dewar, Newman, and Levett-Yeats consented to collaborate in the work.

After a consultation with Mr. Martin Duncan, it was decided to give (1) the names in the 'Fauna of British India,' second edition, by E. C. Stuart Baker, (2) those in the first edition by Blanford and Oates, and (3) those in Jerdon's 'Birds of India.' In addition, a column for any alternative name has been added. Strictly speaking there is no such thing, the name used being either correct or not. Experts, however, often disagree as to whether certain birds should be grouped in one genus or split into separate ones, so it is useful to give both versions. Some of the names in the second edition of the 'Fauna' are incorrectly spelt according to the rules of zoological nomenclature, and in those instances the correct spelling is given in the alternative column.

The English name comes after the scientific names, and then a reference to the

volume, plate, and figure, first in Hodgson, secondly in Tickell, and thirdly in Sharpe. Several of Sharpe's paintings are mounted separately on cardboard, and these are referred to as Mounted Plates abbreviated into M.P. A "dash" indicates that the bird has either not been described or that there is no figure.

In the days of Blanford, Oates, and Tickell subspecies were not recognized, but with modern changes in ornithology these have to be considered. Many of the old species have been given subspecific rank, and many new ones have been created.

As the three authorities quoted worked in different parts of India, the diagnosis of what bird is meant has been comparatively easy, but the only way to make absolutely certain, in some instances, would be by a comparison of the skins in the British Museum (Natural History). This course would have doubled the labour involved in the classification, and has therefore not been adopted.

The classification followed is that used in the Zoological Society's 'List of the Vertebrated Animals,' Centenary Edition, volume ii., Birds. A perusal of the index of that volume will assist those who do not know scientific ornithology to find the names of many of the birds mentioned, or, at any rate, their order and family. A classification of the natural orders is given at the beginning of the List.

Owing to the many changes in ornithological nomenclature that have been made, and may yet be made, the English names of birds have assumed considerable importance as being less unstable than scientific names.

Unfortunately most Indian birds have been saddled with more than one English name.

We hope that the English names here adopted will be used in future by all writers, in order that each bird may acquire a universally accepted English name which will be unaffected by changes in scientific nomenclature.

In consequence of climatic diversity the Indian Empire comprises four well-defined ornithological areas:—(1) the Himalayan, (2) the Peninsular Area (comprising all plains of India), (3) the Nilgiri and Palni Hill Area, (4) the Burmese Area.

The climate of (1) and (3) is temperate, that of (2) and (4) tropical.

The sketch-map appended to show the different areas worked in by the three authorities should prove of use in identifying the species and subspecies, and also help young ornithologists proceeding to India.

It will be seen that Hodgson worked in the Himalayan area, Tickell in the Peninsular and Burmese areas, and Sharpe in the Peninsular, Himalayan, and Nilgiri areas.

Sharpe's pictures are approximately of life size, as are many of Hodgson's. In Tickell the scale is usually given below the picture.

In all 935 species or subspecies have been listed.

Biographical Note.

Brian Houghton Hodgson (1800–1894), Honourable East India Company's Service.

Went to India in 1818. Assistant Commissioner of Kumann, 1818–1820. Assistant Resident at Katmandu (Nepal), 1820–1829. Resident, 1829–1844. Lived at Darjeeling, 1845–1858.

Samuel Richard Tickell, Honourable East India Company, Bengal Army.

Went to India in 1828. Appointed to 31st Regiment of Bengal Infantry Stationed at various places in Lower and Upper Bengal from 1829–1843. Assistant to the Commissioner of Chota Nagpur, 1843–1847. Assistant to the Commissioner of Arracan, 1847–1855. Deputy Commissioner of Tenasserim and Martaban Province at Amherst, 1855. Commissioner of Pegu, 1863–1865. Retired in 1865.

CHARLES FERGUSON SHARPE, Honourable East India Company, Bengal Army.

Went to India in 1850. Appointed to the 72nd Bengal Infantry. Entered Civil employ in 1858, and was appointed Assistant Superintendent of Police in Oudh. He served first as Assistant and then as Superintendent of Police in various districts of Oudh from 1858 to 1891.

Classification of the Natural Orders of Birds.

Class AVES.

Subclass NEORNITHES.

CARINATÆ.

	Page		Page
1. Passeriformes	4	17. Ardeiformes	62
2. Menuriformes	—	18. Balearicifornes	64
3. Eurylaimiformes	42	19. Opisthocomiformes	—
4. Piciformes	42	20. Charadriiformes	64
5. Coccygiformes	46	21. Lariformes	68
6. Trogoniformes	48	22. Alciformes	—
7. Coraciiformes	48	23. Procellariiformes	—
8. Psittaciformes	52	24. Spheniseiformes	—
9. Strigiformes	52	25. Colymbiformes	—
10. Accipitriformes	54	26. Podicipidiformes	68
11. Sagittariiformes	—	27. Ralliformes	70
12. Cathartiformes	—	28. Columbiformes	70
13. Pelecaniformes	60	29. Turniciformes	72
14. Palamedeiformes	—	30. Pterocletiformes	72
15. Phœnicopteriformes	60	31. Galliformes	72
16. Anseriformes	60	32. Mesœniformes	—

The natural orders underlined are absent from the list of paintings.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Order PASSERIFORMES.		
	Family CORVIDÆ.		
	Corvus corax tibetanus.	*Corvus corax.*	*Corvus tibetanus.*
Corvus coronoides levaillantii correct spelling.	*Corvus coronoides levaillanti.*	*Corvus macrorhynchus.*	*Corvus culminatus.*
	Corvus coronoides intermedius.	*Corvus macrorhynchus.*	*Corvus intermedius.*
	Corvus coronoides culminatus.	*Corvus macrorhynchus.*	*Corvus culminatus.*
	Corvus splendens splendens.	*Corvus splendens.*	*Corvus splendens.*
	Nucifraga caryocatactes hemispila.	*Nucifraga hemispila.*	*Nucifraga hemispila.*
	Pica pica bottanensis.	*Pica bottanensis.*	*Pica bottanensis.*
	Urocissa melanocephala occipitalis.	*Urocissa occipitalis.*	*Urocissa sinensis.*
	Urocissa melanocephala magnirostris.	*Urocissa occipitalis.*	*Urocissa sinensis.*
	Urocissa flavirostris flavirostris.	*Urocissa flavirostris.*	*Urocissa flavirostris.*
	Dendrocitta rufa rufa.	*Dendrocitta rufa.*	*Dendrocitta rufa.*
	Dendrocitta rufa vagabunda.	*Dendrocitta rufa.*	*Dendrocitta rufa.*
	Dendrocitta sinensis himalayensis.	*Dendrocitta himalayensis.*	*Dendrocitta sinensis.*
	Dendrocitta sinensis assimilis.	*Dendrocitta himalayensis.*	*Dendrocitta sinensis.*
	Dendrocitta frontalis.	*Dendrocitta frontalis.*	*Dendrocitta frontalis.*
	Dendrocitta leucogastra.	*Dendrocitta leucogastra.*	*Dendrocitta leucogastra.*
	Crypsirhina varians.	*Crypsirhina varians.*	——
	Crypsirhina cucullata.	*Crypsirhina cucullata.*	——
	Cissa chinensis chinensis.	*Cissa chinensis.*	*Cissa sinensis.*
	Garrulus bispecularis bispecularis.	*Garrulus bispecularis.*	*Garrulus bispecularis.*
	Garrulus bispecularis interstinctus.	*Garrulus bispecularis.*	*Garrulus bispecularis.*
	Garrulus lanceolatus.	*Garrulus lanceolatus.*	*Garrulus lanceolatus.*
	Pyrrhocorax pyrrhocorax.	*Graculus eremita.*	*Fregilus himalayanus.*
	Family STURNIDÆ.		
	Sturnus vulgaris humii.	*Sturnus humii.*	*Sturnus unicolor.*
	Sturnus vulgaris subsp. ?	*Sturnus vulgaris.*	*Sturnus vulgaris.*
	Sturnia malabarica malabarica.	*Sturnia malabarica.*	*Temenuchus malabaricus.*
	Sturnia malabarica nemoricola.	*Sturnia nemoricola.*	*Temenuchus malabaricus.*
	Agropsar sturninus.	*Agropsar sturninus.*	——
	Ampeliceps coronatus.	*Ampeliceps coronatus.*	——
	Pastor roseus.	*Pastor roseus.*	*Pastor roseus.*
	Temenuchus pagodarum.	*Temenuchus pagodarum.*	*Temenuchus pagodarum.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Tibet Raven.	iv. pl. 175.	—	—
Indian Jungle Crow.	—	i. fig. 115.	—
Himalayan Jungle Crow.	iv. pl. 176.	—	xii. pl. 70.
Southern Jungle Crow.	—	—	xii. pl. 14.
Indian House Crow.	—	i. fig. 116.	xii. pl. 12.
Himalayan Nutcracker.	iv. pls. 178, 179.	—	vii. pl. 1.
Black-rumped Magpie.	iv. pl. 180.	—	—
Red-billed Blue Magpie.	iv. pls. 185, 186, 187.	—	x. pl. 26.
Burmese Red-billed Blue Magpie.	—	i. fig. 331.	—
Yellow-billed Blue Magpie.	iv. pl. 188.	xi. pl. 5.	xii. pl. 15.
Indian Tree Pie.	—	—	vii. pl. 8.
Bengal Tree Pie.	iv. pl. 192, nest; pl. 193.	—	vii. pl. 10.
Himalayan Tree Pie.	iv. pls. 192, 197, nest; pls. 194, 195.	—	vii. pls. 9, 11, 12.
Burmese Hill Tree Pie.	—	i. fig. 261.	—
Black-browed Tree Pie.	iv. pl. 196.	—	—
Southern Tree Pie.	—	—	xii. pl. 16.
Black Racket-tailed Magpie.	—	i. fig. 262.	—
Hooded Racket-tailed Magpie.	—	ii. fig. 421.	—
Green Magpie.	iv. pls. 189, 190, 191.	i. fig. 114.	vii. pls. 6, 7, x. pl. 26.
Himalayan Jay.	—	—	vii. pl. 3.
Sikkim Jay.	iv. pl. 182.	i. fig. 113.	vii. pl. 2.
Black-throated Jay.	iv. pls. 183, 184.	—	vii. pls. 4, 5, xii. pl. 4.
Red-billed Chough.	iv. pl. 198.	—	—
Himalayan Starling.	iv. pls. 199, 200.	—	—
Indian Starling.	—	x. pl. 12.	vii. pl. 13.
Grey-headed Myna.	iv. pls. 206, 207.	—	vii. pls. 22, 23.
White-winged Myna.	—	i. fig. 268.	—
Daurian Myna.	—	i. fig. 269.	—
Gold-crested Myna.	—	i. fig. 266.	—
Rose-coloured Pastor.	iv. pl. 208.	—	vii. pl. 24.
Black-headed or Brahminy Myna.	iv. pl. 207.	—	vii. pl. 21.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Acridotheres tristis tristis.	*Acridotheres tristis.*	*Acridotheres tristis.*
	Acridotheres ginginianus.	*Acridotheres ginginianus.*	*Acridotheres ginginianus.*
	Æthiopsar fuscus fuscus.	*Æthiopsar fuscus.*	*Acridotheres fuscus*
Sturnopastor contra contra.	*Sturnopastor capensis capensis.*	*Sturnopastor contra.*	*Sturnopastor contra.*
	Family EULABETIDÆ.		
Gracula religiosa.	*Eulabes religiosa.*	*Eulabes religiosa.*	*Eulabes religiosa.*
Gracula javana intermedia.	*Eulabes javana intermedia.*	*Eulabes intermedia.*	*Eulabes intermedia.*
	Lamprocorax panayensis strigatus.	*Calornis chalybeius.*	——
	Saroglossa spiloptera spiloptera.	*Psaroglossa spiloptera.*	*Saraglossa spiloptera.*
	Family DICRURIDÆ.		
	Dicrurus annectens.	*Dicrurus annectens.*	*Dicrurus balicassius.*
	Dicrurus macrocercus macrocercus.	*Dicrurus ater.*	*Dicrurus macrocercus*
	Dicrurus macrocercus albirictus.	*Dicrurus ater.*	*Dicrurus macrocercus.*
	Dicrurus leucophæus longicaudatus.	*Dicrurus longicaudatus.*	*Dicrurus longicaudatus.*
	Dicrurus leucophæus nigrescens.	*Dicrurus nigrescens.*	——
	Dicrurus cærulescens cærulescens.	*Dicrurus cærulescens.*	*Dicrurus cærulescens.*
	Chaptia ænea ænea.	*Chaptia ænea.*	*Chaptia ænea.*
	Chibia hottentotta hottentotta.	*Chibia hottentotta.*	*Chibia hottentotta.*
	Dissemurus paradiseus paradiseus.	*Dissemurus paradiseus.*	*Edolius paradiseus.*
	Dissemurus paradiseus grandis.	*Dissemurus paradiseus.*	*Edolius paradiseus.*
	Dissemurus paradiseus malabaricus.	*Dissemurus paradiseus.*	*Edolius malabaricus.*
	Bhringa remifer tectirostris.	*Bhringa remifer.*	*Bhringa remifer.*
	Family ORIOLIDÆ.		
	Oriolus oriolus kundoo.	*Oriolus kundoo.*	*Oriolus kundoo.*
	Oriolus chinensis tenuirostris.	*Oriolus tenuirostris.*	*Oriolus indicus.*
	Oriolus xanthornus xanthornus.	*Oriolus melanocephalus.*	*Oriolus melanocephalus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Common Myna.	iv. pl. 203.	i. fig. 118.	vii. pls. 15, 16.
Bank Myna.	iv. pl. 204.	——	vii. pl. 17.
Indian Jungle Myna.	iv. pl. 205.	i. fig. 338.	vii. pls. 18, 19, 20.
Indian Pied Myna.	iv. pls. 201, 202.	i. fig. 119.	vii. pl. 14.
Southern Grackle or Hill Myna.	——	——	vii. pl. 26.
Indian Grackle or Hill Myna.	iv. pl. 211.	i. fig. 337.	vii. pl. 27.
Glossy Starling or Stare.	——	i. fig. 267.	—
Spotted-winged Stare.	iv. pls. 209, 210.	——	vii. pl. 25.
Crow-billed Drongo.	iii. pls. 51, 52.	vii. pl. 15.	——
Black Drongo or King Crow.	——	vii. pl. 14.	iii. pl. 39.
Himalayan Black Drongo.	iii. pls. 48, 49, 50.	——	——
Indian Grey Drongo.	iii. pl. 52.	——	iii. pls. 40, 41.
Burmese Grey Drongo.	——	vii. pl. 17.	——
White-bellied Drongo.	iii. pl. 53.	vii. pl. 16.	iii. pl. 41.
Northern Bronzed Drongo.	iii. pls. 54, 55, 56.	vii. pl. 18.	iii. pl. 42.
Indian Hair-crested Drongo.	iii. pls. 59, 60, 61.	vii. pl. 21.	——
Siam Large Racket-tailed Drongo or Bhimraj.	——	i. fig. 285; vii. pl. 20.	——
Assam Large Racket-tailed Drongo or Bhimraj.	iii. pl. 58.	——	x. pl. 27, left figure.
Malabar Large Racket-tailed Drongo or Bhimraj.	——	——	iii. pl. 42.
Indian Lesser Racket-tailed Drongo.	iii. pl. 57.	vii. pl. 19.	x. pl. 27, right figure.
Indian Oriole.	iv. pls. 19, 20, 21, 26.	vi. pl. 27.	v. pls. 24, 25, xii. pl. 17, figs. 1, 2.
Burmese Black-naped Oriole.	——	i. fig. 187; vi. pl. 28.	——
Indian Black-headed Oriole.	iv. pls. 21, 22, 23.	ii. fig. 64; vi. pl. 29.	v. pl. 26, xii. pl. 17, figs. 3 & 4.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Oriolus xanthornus ceylonensis.	*Oriolus melanocephalus.*	*Oriolus ceylonensis.*
Oriolus traillii traillii.	*Oriolus traillii.*	*Oriolus traillii.*	*Oriolus traillii.*
	Family PLOCEIDÆ.		
	Stictospiza formosa.	*Stictospiza formosa.*	*Estrelda formosa.*
	Amandava amandava.	*Sporæginthus amandava.*	*Estrelda amandava.*
	Munia malacca orientalis.	*Munia malacca.*	*Munia malacca.*
	Munia atricapilla atricapilla.	*Munia atricapilla.*	*Munia rubronigra.*
	Munia atricapilla rubronigra.	*Munia atricapilla.*	*Munia rubronigra.*
Munia punctulata punctulata.	*Uroloncha punctulata punctulata.*	*Uroloncha punctulata.*	*Munia undulata.*
Munia striata striata.	*Uroloncha striata striata.*	*Uroloncha striata.*	*Munia striata.*
Munia striata acuticauda.	*Uroloncha striata acuticauda.*	*Uroloncha acuticauda.*	*Munia acuticauda.*
Munia malabarica.	*Uroloncha malabarica.*	*Uroloncha malabarica.*	*Munia malabarica.*
	Ploceus philippinus.	*Ploceus baya.*	*Ploceus baya.*
Ploceus philippinus passerinus.	*Ploceus passerinus passerinus.*	*Ploceus megarhynchus.*	*Ploceus baya.*
	Ploceus benghalensis.	*Ploceus bengalensis.*	*Ploceus bengalensis.*
	Ploceus manyar peguensis.	*Ploceus manyar.*	*Ploceus manyar.*
	Family FRINGILLIDÆ.		
Mycerobas melanoxanthos.	*Mycerobas melanoxanthus.*	*Mycerobas melanoxanthus.*	*Mycerobas melanoxanthos.*
	Perissospiza icterioides affinis.	*Pycnorhamphus affinis.*	*Hesperiphona affinis.*
	Perissospiza carnipes.	*Pycnorhamphus carneipes.*	*Mycerobas carnipes.*
	Carduelis caniceps caniceps.	*Carduelis caniceps.*	*Carduelis caniceps.*
Hypacanthis spinoïdes spinoïdes correct spelling.	*Hypacanthis spinoides spinoides.*	*Hypacanthis spinoides.*	*Chrysomitris spinoides.*
	Gymnoris xanthocollis xanthocollis.	*Gymnorhis flavicollis.*	*Passer flavicollis.*
	Passer domesticus indicus.	*Passer domesticus.*	*Passer indicus.*
	Passer montanus malaccensis.	*Passer montanus.*	*Passer montanus.*
	Passer rutilans cinnamomeus.	*Passer cinnamomeus.*	*Passer cinnamomeus.*
Haematospiza indica.	*Hæmatospiza sipahi.*	*Hæmatospiza sipahi.*	*Hæmatospiza sipahi.*
	Carpodacus erythrinus roseatus.	*Carpodacus erythrinus.*	*Carpodacus erythrinus.*
	Propyrrhula subhimachala subhimachala.	*Propyrrhula subhimalayensis.*	*Propyrrhula subhimachala.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Ceylon Black-headed Oriole.	——	——	v. pl. 27.
Maroon Oriole.	iv. pls. 22, 23, 24, 25, 26.	vi. pl. 30.	v. pl. 28, xii. pl. 17, fig. 5.
Green Munia or Waxbill.	——	——	vii. pl. 35.
Avadavat or Indian Red Munia.	v. pl. 6.	——	vii. pls. 34, 35
Madras Black-headed Munia.	——	——	vii. pl. 30.
Malay Chestnut-bellied Munia.	——	ii. fig. 376.	——
Northern Chestnut-bellied Munia.	v. pls. 2, 4.	——	——
Indian Spotted Munia.	v. pls. 2, 5.	i. fig. 272.	vii. pl. 31.
White-backed Munia.	——	——	vii. pl. 32.
Hodgson's Munia.	v. pl. 2.	ii. fig. 395.	vii. pl. 33.
White-throated Munia.	v. pl. 2.	——	vii. pl. 33.
Baya or Weaver-Bird.	——	i. fig. 270.	vii. pl. 28.
Eastern Baya.	v. pl. 1.	ii. fig. 420.	——
Black-throated Weaver-Bird.	v. pl. 1.	i. fig. 120.	vii. pl. 29.
Burmese Striated Weaver-Bird.	——	i. fig. 271.	——
Spotted-winged Grosbeak.	v. pls. 2, 21, 22.	——	vii. pl. 48.
Allied or Eastern Black-and-Yellow Grosbeak	v. pl. 20.	——	——
White-winged Grosbeak.	v. pls. 2, 23.	——	——
Himalayan Goldfinch.	——	——	vii. pl. 61.
Himalayan Greenfinch.	v. pls. 13, 33, nest; pl. 39, 40.	——	vii. pls. 53. 62, 63.
Yellow-throated Sparrow.	v. pl. 11.	i. fig. 121.	vii. pls. 39, 40.
Indian House-Sparrow.	v. pls. 7, 8, 36.	i. fig. 135.	vii. pl. 39.
Malay or Indian Tree-Sparrow.	v. pls. 7, 8, 10.	——	vii. pl. 38.
Cinnamon Tree-Sparrow.	v. pl. 9.	ii. fig. 424.	vii. pls. 36, 37.
Scarlet Finch.	v. pls. 21, 28, 29.	i. fig. 123.	vii. pls. 52, 54.
Indian Rose-Finch.	v. pls. 31, 34. 35, 36.	i. fig. 122.	vii. pls. 55, 56, 57.
Red-headed Rose-Finch.	v. pls. 28, 30.	——	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Propasser rhodochrous.	*Propasser rhodochrous.*	*Propasser rhodochrous.*
	Propasser rodopeplus.	*Propasser rhodopeplus.*	*Propasser rodopeplus.*
	Procarduelis nipalensis nipalensis.	*Procarduelis nepalensis.*	*Procarduelis nipalensis.*
	Pyrrospiza punicea punicea.	*Pyrrospiza punicea.*	*Pyrrospiza punicea.*
Loxia curvirostra himalayensis.	*Loxia curvirostra himalayana.*	*Loxia himalayana.*	*Loxia himalayana.*
	Pyrrhula nipalensis nipalensis.	*Pyrrhula nepalensis.*	*Pyrrhula nipalensis.*
	Pyrrhula erythrocephala.	*Pyrrhula erythrocephala.*	*Pyrrhula erythrocephala.*
	Pyrroplectes epauletta.	*Pyrroplectes epauletta.*	*Pyrroplectes epauletta.*
	Fringillauda nemoricola nemoricola.	*Fringillauda nemoricola.*	*Fringillauda nemoricola.*
	Emberiza fucata arcuata.	*Emberiza fucata.*	*Emberiza fucata.*
	Emberiza pusilla.	*Emberiza pusilla.*	*Emberiza pusilla.*
	Emberiza stewarti.	*Emberiza stewarti.*	*Emberiza stewarti.*
	Emberiza aureola.	*Emberiza aureola.*	*Euspiza aureola.*
	Emberiza icterica.	*Emberiza luteola.*	*Euspiza lutcola.*
	Melophus melanicterus.	*Melophus melanicterus.*	*Melophus melunicterus.*
	Family ALAUDIDÆ.		
	Melanocorypha bimaculata bimaculata.	*Melanocorypha bimaculata.*	——
	Alauda arvensis dulcivox.	*Alauda arvensis.*	*Alauda triborhyncha.*
	Alauda gulgula gulgula.	*Alauda gulgula.*	*Alauda gulgula.*
	Calandrella brachydactyla dukhunensis.	*Calandrella dukhunensis.*	*Calandrella brachydactyla.*
	Mirafra cantillans cantillans.	*Mirafra cantillans.*	*Mirafra cantillans.*
	Mirafra assamica assamica.	*Mirafra assamica.*	*Mirafra assamica.*
	Mirafra erythroptera erythroptera.	*Mirafra erythroptera.*	*Mirafra erythroptera.*
	Galerida cristata chendoola.	*Galerita cristata.*	*Galerida cristata.*
Eremopterix grisea.	*Pyrrulauda grisea.*	*Pyrrulauda grisea.*	*Pyrrulauda grisea.*
	Family MOTACILLIDÆ.		
	Motacilla alba dukhunensis.	*Motacilla alba.*	*Motacilla dukhunensis.*
	Motacilla alba personata.	*Motacilla personata.*	*Motacilla dukhunensis.*
Motacilla alba alboides.	*Motacilla lugubris alboides.*	*Motacilla hodgsoni.*	*Motacilla luzoniensis.*
Motacilla alba leucop-	*Motacilla lugubris leucopsis.*	*Motacilla leucopsis.*	*Motacilla luzoniensis.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Pink-browed Rose-Finch.	v. pl. 33.	——	vii. pl. 58.
Spotted-winged Rose-Finch.	v. pl. 32.	——	——
Nepal Dark Rose-Finch.	v. pls. 31, 37.	——	vii. pl. 59.
Red-breasted Rose-Finch.	v. pl. 38.	——	vii. pl. 60.
Himalayan Crossbill.	v. pl. 27.	——	——
Brown Bullfinch.	v. pl. 24.	——	vii. pls. 49, 50.
Red-headed Bullfinch.	v. pl. 24.	——	——
Gold-headed Black Finch.	v. pl. 31.	——	vii. pls. 51, 53.
Hodgson's Mountain Finch.	v. pl. 41.	——	——
Grey-headed Bunting.	v. pl. 14.	——	vii. pl. 46.
Little Bunting.	v. pl. 15.	——	vii. pl. 42.
White-capped Bunting.	——	——	vii. pl. 41.
Yellow-breasted Bunting.	v. pl. 17.	i. fig. 273.	——
Red-headed Bunting.	——	——	vii. pls. 43, 44.
Crested Bunting.	v. pls. 18, 19.	ii. fig. 431.	vii. pls. 45, 46, 47.
Eastern Calandra Lark.	——	——	vii. pls. 65, 66.
Eastern Sky-Lark.	v. pls. 46, 47.	——	——
Small Indian Sky-Lark.	——	——	vii. pls. 67, 68.
Rufous Short-toed Lark.	v. pls. 15, 45.	i. fig. 247.	vii. pl. 68.
Singing Bush-Lark.	——	i. fig. 245.	——
Bengal Bush-Lark.	——	i. fig. 246.	vii. pl. 64.
Red-winged Bush-Lark.	——	——	vii. pl. 65.
Franklin's Crested Lark.	v. pl. 48.	——	vii. pl. 69.
Ashy Crowned Finch-Lark.	v. pl. 42.	i. fig. 248.	vii. pl. 68.
Indian White Wagtail.	iv. pl. 103, figs. 2, 5.	i. fig. 139.	——
Masked Wagtail.	iv. pl. 103, fig. 6.	——	——
Hodgson's Pied Wagtail.	iv. pl. 103, figs. 1, 3; pl. 104.	——	——
White-faced Wagtail.	——	i. fig. 139.	vi. pl. 7.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Motacilla maderaspatensis.	*Motacilla lugubris maderaspatensis.*	*Motacilla maderaspatensis.*	*Motacilla maderaspatana.*
	Motacilla cinerea caspica.	*Motacilla melanope.*	*Culobates sulphurea.*
	Motacilla flava thunbergi.	*Motacilla borealis.*	*Budytes viridis.*
	Motacilla flava beema.	*Motacilla beema.*	——
	Motacilla citreola citreola.	*Motacilla citreola.*	*Budytes citreola.*
	Motacilla citreola calcarata.	*Motacilla citreoloides.*	*Budytes citreola.*
	Dendronanthus indicus.	*Limonidromus indicus.*	*Nemoricola indica.*
	Anthus trivialis trivialis.	*Anthus trivialis.*	*Pipastes arboreus.*
	Anthus hodgsoni hodgsoni.	*Anthus maculatus.*	*Pipastes agilis.*
	Anthus richardi richardi.	*Anthus richardi.*	*Corydalla richardi.*
	Anthus richardi rufulus.	*Anthus rufulus.*	*Corydalla rufula.*
Anthus richardi striolatus.	*Anthus richardi godlewskii.*	*Anthus striolatus.*	*Corydalla striolata.*
	Anthus nilghiriensis.	*Anthus nilghiriensis.*	*Pipastes montanus.*
	Anthus campestris campestris.	*Anthus campestris.*	*Agrodroma campestris.*
	Anthus roseatus.	*Anthus rosaceus.*	*Anthus cervinus.*
	Anthus sordidus jerdoni.	*Anthus similis.*	*Agrodroma sordida.*
	Oreocorys sylvanus.	*Oreocorys sylvanus.*	*Heterura sylvana.*
	Family NECTARINIIDÆ.		
	Chalcoparia singalensis singalensis.	*Chalcoparia phœnicotis.*	——
	Æthopyga siparaja seheriæ.	*Æthopyga seheriæ.*	*Æthopyga miles.*
	Æthopya ignicauda ignicauda.	*Æthopyga ignicauda.*	*Æthopyga ignicauda.*
	Æthopyga gouldiæ gouldiæ.	*Æthopyga gouldiæ.*	*Æthopyga gouldiæ.*
	Æthopyga saturata saturata.	*Æthopyga saturata.*	*Æthopyga saturata.*
	Æthopyga nipalensis nipalensis.	*Æthopyga nepalensis.*	*Æthopyga nipalensis.*
Cyrtostomus asiaticus asiaticus.	*Leptocoma asiatica asiatica.*	*Arachnechthra asiatica.*	*Arachnechthra asiatica.*
	Leptocoma minima.	*Arachnechthra minima.*	*Leptocoma minima.*
	Leptocoma zeylonica.	*Arachnechthra zeylonica.*	*Leptocoma zeylonica.*
	Leptocoma lotenia.	*Arachnechthra lotenia.*	*Arachnechthra lotenia.*
	Leptocoma brasiliana.	*Arachnechthra hasselti.*	——

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Large Pied Wagtail.	iv. pl. 106.	——	vi. pls. 5, 6, 7.
Eastern Grey Wagtail.	iv. pl. 103, fig. 4; pl. 107, fig. 3; pl. 108.	——	vi. pl. 7.
Grey-headed Wagtail.	iv. pl. 113, figs. 3, 4; pl. 114, figs. 5, 6.	i. fig. 141.	vi. pl. 7, ? 8.
Indian Blue-headed Wagtail.	iv. pl. 112.	——	——
Yellow-headed Wagtail.	——	i. fig. 140.	vi. pl. 9.
Hodgson's Yellow-headed Wagtail.	iv. pl. 114, fig. 1; pl. 115, figs. 1, 2; pl. 116, young bird.	——	——
Forest Wagtail.	——	i. fig. 305.	——
Tree Pipit.	——	i. fig. 138.	——
Indian Tree-Pipit.	iv. pls. 117, 119, 123, fig. 4.	——	vi. pls. 10, 11.
Richard's Pipit.	iv. pl. 118.	——	vi. pl. 12.
Indian Pipit.	iv. pls. 120, 122, figs. 2, 3.	i. fig. 137.	vi. pls. 13, 14.
Blyth's Pipit.	iv. pls. 121, 122, figs. 1, 4.	i. fig. 136.	vi. pls. 14, 15, 16, 17.
Nilgiri Pipit.	——	——	vi. pl. 11.
Tawny Pipit.	——	——	vi. pl. 10.
Hodgson's Pipit.	iv. pls. 123, 124, 125.	——	——
Brown Rock-Pipit.	——	——	vi. pls. 17, 18.
Upland Pipit.	iv. pl. 126.	——	vi. pl. 19.
Malayan Ruby Cheek.	——	ii. fig. 429; vi. pl. 16.	——
Himalayan Yellow-backed Sunbird.	iii. pl. 1, fig. 6; pl. 3, fig. 7; pl. 4; pl. 5, fig. 3; pl. 6.	ii. fig. 429; vi. pl. 7.	ii. pls. 67, 68.
Fire-tailed Yellow-backed Sunbird.	iii. pl. 3, figs. 1, 4, 8; pl. 5, figs. 6, 7.	vi. pl. 9.	ii. pls. 65, 67.
Mrs. Gould's Yellow-backed Sunbird.	——	vi. pl. 8.	——
Black-breasted Sunbird.	iii. pl. 1, fig. 5; pl. 5, fig. 8; pl. 8.	vi. pl. 11.	ii. pls. 66, 67, 68.
Nepal Yellow-backed Sunbird.	iii. pl. 1, fig. 6; pl. 3, figs. 2, 3; pl. 5, figs. 9, 10; pl. 7.	vi. pl. 10.	ii. pls. 69, 72.
Purple Sunbird.	iii. pl. 1, fig. 1; pl. 5, fig. 5; pl. 9.	vi. pl. 12.	ii. pls. 70, 72.
Small Sunbird.	——	——	ii. pl. 71.
Purple-rumped Sunbird.	——	vi. pl. 13.	——
Loten's Sunbird.	——	——	ii. pl. 73.
Van Hasselt's Sunbird.	——	i. fig. 168; vi. pl. 15.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Leptocoma flammaxillaris flammaxillaris.	*Arachnechthra flammaxillaris.*	——
	Arachnothera magna magna.	*Arachnothera magna.*	*Arachnothera magna.*
	Family DICÆIDÆ.		
	Dicæum cruentatum cruentatum.	*Dicæum cruentatum.*	*Dicæum coccineum.*
	Dicæum cruentatum ignitum.	*Dicæum cruentatum.*	*Dicæum coccineum.*
	Dicæum chrysorrheum intensum.	*Dicæum chrysorrhœum.*	*Dicæum chrysorrhœum.*
	Dicæum chrysorrheum chrysochlore.	*Dicæum chrysorrhœum.*	*Dicæum chrysorrhœum.*
	Dicæum trigonostigma rubropygium.	*Dicæum trigonostigma.*	——
	Dicæum ignipectum ignipectum.	*Dicæum ignipectus.*	——
	Dicæum minullum concolor.	*Dicæum concolor.*	*Dicæum concolor.*
Dicæum erythrorhynchos erythrorhynchos.	*Dicæum erythrorhynchum erythrorhynchum.*	*Dicæum erythrorhynchus.*	*Dicæum minimum.*
	Piprisoma squalidum squalidum.	*Piprisoma squalidum.*	*Piprisoma agile.*
	Pachyglossa melanoxantha.	*Pachyglossa melanoxantha.*	*Pachyglossa melanoxantha.*
	Family ZOSTEROPIDÆ.		
	Zosterops palpebrosa palpebrosa.	*Zosterops palpebrosa.*	*Zosterops palpebrosus.*
	Family CERTHIIDÆ.		
	Certhia himalayana himalayana.	*Certhia himalayana.*	*Certhia himalayana.*
	Certhia familiaris nipalensis.	*Certhia nepalensis.*	*Certhia nipalensis.*
	Certhia familiaris hodgsoni.	*Certhia hodgsoni.*	——
	Certhia discolor discolor.	*Certhia discolor.*	*Certhia discolor.*
	Tichodroma muraria.	*Tichodroma muraria.*	*Tichodroma muraria.*
	Family SITTIDÆ.		
	Sitta himalayensis.	*Sitta himalayensis.*	*Sitta himalayensis.*
Sitta castaneoventris castaneoventris correct spelling.	*Sitta castaneiventris castaneiventris.*	*Sitta castaneiventris.*	*Sitta castaneoventris.*

English Name.	Hodgson.	Tickell.	C. F Sharpe.
Burmese Yellow-breasted Sunbird.	——	vi. pl. 14. (Under *Nectarinia jugularis*.)	——
Indian Streaked Spider-Hunter.	iii. pl. 1, fig. 4; pl. 2; pl. 5, fig. 4.	vi. pl. 6.	ii. pl. 64.
Indian Scarlet-backed Flower-pecker.	iii. pl. 10.	——	iii. pl. 2.
Burmese Scarlet-backed Flower-pecker.	——	i. fig. 169; vi. pl. 17.	——
Sikkim Yellow-vented Flower-pecker.	iii. pl. 12.	——	iii. pl. 2.
Burmese Yellow-vented Flower-pecker.	——	ii. fig. 408, no. 3; vi. pls. 17, 18 (wrongly described in latter plate as *Pipriosoma agilis*).	——
Tenasserim Orange-bellied Flower-pecker.	——	ii. fig. 408, no. 2; vi. pl. 18, fig. 2.	——
Fire-breasted Flower-pecker.	iii. pl. 15; iv. pl. 157, fig. 6.	——	iii. pls. 1, 2.
Nilgiri Flower-pecker.	——	——	iii. pl. 3.
Tickell's Flower-pecker.	iii. pl. 12, figs. 1, 2; pl. 14.	ii. fig. 408, no. 1; vi. pl. 17, fig. 1.	iii. pl. 1.
Thick-billed Flower-pecker.	——	vi. pl. 18, fig. 1.	iii. pl. 1.
Yellow-bellied Flower-pecker.	iii. pl. 17.	——	iii. pl. 4.
Indian White Eye.	iv. pls. 157, fig. 2, 159.	ii. fig. 393; vi. pl. 19.	vi. pl. 41.
Himalayan Tree-Creeper.	——	——	iii. pl. 5.
Nepal Tree-Creeper.	iii. pl. 18.	——	iii. pl. 5.
Hodgson's Tree-Creeper.	——	——	iii. pl. 5 (bottom right-hand figure)
Sikkim Tree-Creeper.	——	vi. pl. 1; xi. pl. 12.	iii. pl. 5.
Wall-Creeper.	iii. pls. 19, 20.	——	——
White-tailed Nuthatch.	iii. pl. 21; iv. pls. 166, 167.	vi. pl. 4.	iii. pls. 6, 8.
Chestnut-bellied Nuthatch.	iv. pls. 166, 167, fig. 3.	vi. pl. 3, fig. 1.	iii. pl. 8.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st. Ed.	Jerdon.
	Sitta castaneiventris cinnamoventris.	*Sitta cinnamomeiventris.*	*Sitta cinnamomeoventris.*
	Sitta formosa.	*Sitta formosa.*	*Sitta formosa.*
	Sitta frontalis frontalis.	*Sitta frontalis.*	*Dendrophila frontalis.*
	Family REGULIDÆ.		
	Cephalopyrus flammiceps.	*Cephalopyrus flammiceps.*	*Cephalopyrus flammiceps.*
	Family PARIDÆ.		
	Parus major cinereus.	*Parus atriceps.*	*Parus cinereus.*
	Parus major mahrattarum.	——	——
	Parus monticolus monticolus.	*Parus monticolus.*	*Parus monticolus.*
	Lophophanes ater æmodius.	*Lophophanes æmodius.*	*Parus æmodius.*
	Lophophanes rubidiventris.	*Lophophanes rubidiventris.*	*Lophophanes rubidiventris.*
	Lophophanes rufonuchalis beavani.	*Lophophanes beavani.*	*Lophophanes beavani.*
	Lophophanes dichrous dichrous.	*Lophophanes dichrous.*	*Lophophanes dichrous.*
	Sylviparus modestus modestus.	*Sylviparus modestus.*	*Sylviparus modestus.*
	Machlolophus spilonotus spilonotus.	*Machlolophus spilonotus.*	*Machlolophus spilinotus.*
	Machlolophus spilonotus subviridis.	*Machlolophus spilonotus.*	*Machlolophus spilinotus.*
	Machlolophus xanthogenys xanthogenys.	*Machlolophus xantho genys.*	*Machlolophus xanthogenys.*
	Machlolophus xanthogenys aplonotus.	*Machlolophus haplonotus.*	*Machlolophus jerdoni.*
	Ægithaliscus concinnus iredalei.	*Ægithaliscus erythrocephalus.*	*Ægithaliscus erythrocephalus.*
	Ægithaliscus niveogularis.	*Ægithaliscus niveogularis.*	*Ægithaliscus niveogularis.*
	Ægithaliscus ioschistos.	*Ægithaliscus ioschistus.*	*Ægithaliscus iouschistos.*
	Melanochlora sultanea sultanea.	*Melanochlora sultanea.*	*Melanochlora sultanea.*
	Family LANIIDÆ.		
	Lanius excubitor lahtora.	*Lanius lahtora.*	*Lanius lahtora.*
	Lanius vittatus.	*Lanius vittatus.*	*Lanius hardwickii.*
	Lanius collurioides.	*Lanius collurioides.*	——
	Lanius nigriceps nigriceps.	*Lanius nigriceps.*	*Lanius nigriceps.*
	Lanius schach erythronotus.	*Lanius erythronotus.*	*Lanius erythronotus.*
	Lanius schach caniceps.	*Lanius erythronotus.*	*Lanius erythronotus.*
	Lanius tephronotus.	*Lanius tephronotus.*	*Lanius tephronotus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe
Cinnamon-bellied Nuthatch.	iii. pl. 22.	vi. pl. 3, fig. 2.	iii. pl. 8.
Beautiful Nuthatch.	——	i. fig. 45; vi. pl. 2.	——
Velvet-fronted Nuthatch.	iii. pl. 23; iv. pls. 166, 167.	vi. pl. 5.	iii. pls. 7, 8.
Fire-capped Tit-Warbler.	——	——	vi. pl. 44.
Indian Grey Tit.	iv. pl. 164.	——	vi. pl. 51.
Southern Grey Tit.	——	——	vi. pl. 50.
Green-backed Tit.	iv. pls. 165, 166, 167.	x. pl. 35.	vi. pl. 51.
Himalayan Coal Tit.	iv. pl. 162, fig. 1; pl. 164, fig. 2.	——	——
Rufous-bellied Crested Tit.	iv. pl. 162, fig. 4.	——	——
Sikkim Black Tit.	iv. pl. 163.	——	vi. pl. 49.
Brown crested Tit.	iv. pl. 162, fig. 3.	——	vi. pl. 48.
Yellow-browed Tit.	iv. pl. 160; pl. 162, fig. 5.	——	vi. pls. 42, 43.
Northern Black-spotted Yellow Tit.	iv. pl. 168.	——	vi. pls. 53, 54.
Burmese Black-spotted Yellow Tit.	——	i. fig. 336; ii. fig. 428 *a*.	——
Northern Yellow-cheeked Tit.	iv. pl. 166, fig. 2; pl. 167, fig. 1.	——	vi. pl. 53.
Southern Yellow-cheeked Tit.	——	——	vi. pl. 52.
Red-headed Tit.	——	i. fig. 134.	vi. pl. 45.
White-throated Tit.	——	——	vi. pl. 47.
Rufous-fronted Tit.	iv. pl. 162, fig. 2.	——	vi. pl. 46.
Indian Sultan Tit.	iv. pl. 169, figs. 2, 3.	i. fig. 117.	vi. pl. 55.
Indian Grey Shrike.	——	vii. pl. 8.	iii. pl. 10.
Bay-backed Shrike.	iii. pl. 25, fig. 2.	vii. pl. 11.	iii. pls. 16, 17, 18.
Burmese Shrike.	——	i. fig. 309; vii. pl. 12.	——
Indian Black-headed Shrike.	iii. pls. 28, 29, 30, fig. 3.	vii. pl. 10.	iii. pls. 14, 15.
Rufous-backed Shrike.	iii. pls. 25, 32, fig. 3.	vii. pl. 9.	——
Southern Rufous-backed Shrike.	——	——	iii. pls. 11, 19 (upper figure).
Grey-backed Shrike.	iii. pls. 26, 27: iv. pl. 137, fig. 1.	——	iii. pls. 12, 13.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Lanius cristatus cristatus.	*Lanius cristatus.*	*Lanius cristatus.*
	Lanius cristatus isabellinus.	*Lanius isabellinus.*	*Lanius arenarius.*
	Hemipus picatus picatus.	*Hemipus picatus.*	*Hemipus picatus.*
	Tephrodornis pelvica pelvica.	*Tephrodornis pelvicus.*	*Tephrodornis pelvica.*
	Tephrodornis pelvica sylvicola.	*Tephrodornis sylvicola.*	*Tephrodornis sylvicola.*
	Tephrodornis pondiceriana pondiceriana.	*Tephrodornis pondicerianus.*	*Tephrodornis pondiceriana.*
	Family ARTAMIDÆ.		
	Artamus fuscus.	*Artamus fuscus.*	*Artamus fuscus.*
	Family SYLVIIDÆ.		
	Acrocephalus stentoreus brunnescens.	*Acrocephalus stentoreus.*	*Acrocephalus brunnescens.*
	Acrocephalus arundinaceus orientalis.	*Acrocephalus orientalis.*	——
	Acrocephalus dumetorum.	*Acrocephalus dumetorum.*	*Acrocephalus dumetorum.*
	Tribura luteoventris.	*Tribura luteiventris.*	*Tribura luteoventris.*
	Tribura thoracica thoracica.	*Tribura thoracica.*	*Horornis flaviventris.*
	Orthotomus sutorius sutorius.	*Orthotomus sutorius.*	*Orthotomus longicauda.*
	Orthotomus sutorius patia.	*Orthotomus sutorius.*	*Orthotomus longicauda.*
	Cisticola juncidis cursitans.	*Cisticola cursitans.*	*Cisticola schœnicola.*
	Franklinia gracilis.	*Franklinia gracilis.*	*Prinia hodgsoni.*
	Franklinia buchanani.	*Franklinia buchanani.*	*Franklinia buchanani.*
	Franklinia cinereocapilla.	*Franklinia cinereicapilla.*	*Prinia cinereocapilla.*
	Megalurus palustris.	*Megalurus palustris.*	*Megalurus palustris.*
	Phragmaticola aëdon.	*Arundinax aëdon.*	*Arundinax olivaceus.*
	Sylvia curruca affinis.	*Sylvia affinis.*	*Sylvia curruca.*
	Phylloscopus affinis.	*Phylloscopus affinis.*	*Phylloscopus affinis.*
	Phylloscopus proregulus newtoni.	*Phylloscopus proregulus.*	*Reguloides chloronotus.*
Phylloscopus humei præmium.	*Phylloscopus humii præmium.*	*Phylloscopus superciliosus.*	*Reguloides proregulus.*
	Phylloscopus collybitus tristis.	*Phylloscopus tristis.*	*Phylloscopus tristis.*
	Phylloscopus fuliginiventer.	*Phylloscopus fuliginiventris.*	*Horornis fuliginiventer.*
	Phylloscopus pulcher pulcher.	*Phylloscopus pulcher.*	*Reguloides erochroa.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Brown Shrike.	iii. pls. 31, 32, fig. 5.	vii. pl. 13.	iii. pls. 19 (lower figure), 20.
Pale Brown Shrike.	——	——	iii. pl. 21.
Black-backed Pied Shrike.	——	vii. pl. 24.	iii. pls. 24, 25.
Nepal Wood-Shrike.	iii. pl. 30, figs 1, 2; pl. 32, figs. 1, 2.	vii. pl. 23.	iii. pl. 22.
Malabar Wood-Shrike.	——	——	iii. pl. 23.
Indian Common Wood-Shrike.	iii. pl. 32, fig. 4.	vii. pl. 22.	iii. pl. 24.
Ashy Swallow-Shrike.	iii. pl. 62.	vii. pl. 1.	iii. pl. 43.
Indian Great Reed-Warbler.	iv. pl. 60, fig. 1.	——	v. pl. 52 (lower figure).
Eastern Great Reed-Warbler.	——	ii. fig. 430. ? under name of *Acrocephalus obscurus*.	——
Blyth's Reed-Warbler.	iv. pls. 61, 62, 63.	——	——
Brown Bush-Warbler.	iv. pl. 64.	——	——
Spotted Bush-Warbler.	iv. pl. 65, figs. 1, 3.	——	——
Indian Tailor Bird.	——	——	v. pl. 60.
Burmese Tailor Bird.	iv. pls. 70, 71.	ii. fig. 416.	——
Streaked Fantail Warbler.	iv. pl. 73.	——	v. pl. 53 (lower figure)
Franklin's Wren-Warbler.	——	——	v. pl. 53.
Rufous-fronted Wren-Warbler.	iv. pl. 68.	——	v. pl. 60.
Hodgson's Wren-Warbler.	iv. pl. 72.	——	——
Striated Marsh-Warbler.	——	i. fig. 109; xi. pl. 23.	iv. pl. 88.
Thick-billed Warbler.	——	i. fig. 310.	v. pl. 52 (upper figure).
Indian Lesser Whitethroat.	——	——	v. pls. 66, 71.
Tickell's Willow-Warbler.	iv. pls. 86, fig. 3; 87	ii. fig. 350.	v. pls. 61, 63, 64.
Pallas's Willow-Warbler, or Yellow-rumped Willow-Warbler.	iv. pls. 86, fig. 5; 88.	——	v. pls. 61 ?, 65.
Crowned Willow-Warbler.	——	——	v. pl. 61.
Brown Willow-Warbler.	——	——	v. pl. 62
Smoky Willow-Warbler.	iv. pl. 65, fig. 2.	——	——
Nepal Orange-barred Willow-Warbler.	iv. pls. 85, fig. 3; 157, fig. 9.	——	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Phylloscopus griseolus griseolus.	*Phylloscopus griseolus.*	*Phylloscopus indicus.*	*Phylloscopus indicus.*
	Acanthopneuste nitidus nitidus.	*Acanthopneuste nitidus.*	*Phylloscopus viridanus.*
	Acanthopneuste magnirostris.	*Acanthopneuste magnirostris.*	*Phylloscopus magnirostris.*
Acanthopneuste trochiloides.	*Acanthopneuste lugubris.*	*Acanthopneuste lugubris.*	*Phylloscopus lugubris.*
	Acanthopneuste occipitalis occipitalis.	*Acanthopneuste occipitalis.*	*Reguloides occipitalis.*
Acanthopneuste reguloides reguloides.	*Acanthopneuste trochiloides trochiloides.*	*Acanthopneuste trochiloides.*	*Reguloides trochiloides.*
			Reguloides viridipennis.
	Seicercus affinis.	*Cryptolopha affinis.*	*Abrornis affinis.*
	Seicercus burkii burkii.	*Crytolopha burkii.*	*Culicipeta burkii.*
Seicercus xanthoschistos xanthoschistos.	*Seicercus xanthoschistus xanthoschistus.*	*Cryptolopha jerdoni.*	*Abrornis xanthoschistos.*
	Seicercus xanthoschistus olbosuperciliaris.	*Cryptolopha xanthoschista.*	*Abrornis albosuperciliaris.*
	Seicercus poliogenys.	*Cryptolopha poliogenys.*	*Abrornis poliogenys.*
	Seicercus castaneoceps castaneoceps.	*Cryptolopha castaneiceps.*	*Abrornis castaneoceps.*
	Abrornis superciliaris superciliaris.	*Abrornis superciliaris.*	*Abrornis flaviventris.*
	Abrornis superciliaris salvinensis.	*Abrornis superciliaris.*	*Abrornis flaviventris.*
	Abrornis schisticeps schisticeps.	*Abrornis schisticeps.*	*Abrornis schisticeps.*
	Tickellia hodgsoni.	*Tickellia hodgsoni.*	*Tickellia hodgsoni.*
	Neornis flavolivaceus flavolivaceus.	*Neornis flavolivaceus.*	*Neornis flavolivacea.*
	Horornis fortipes fortipes.	*Horornis fortipes.*	*Horornis fortipes.*
Horornis pallida pallida correct spelling.	*Horornis pallidus pallidus.*	*Horornis pallidus.*	——
	Horeites brunnifrons.	*Horeites brunneifrons.*	*Horeites brunneifrons.*
	Suya crinigera crinigera.	*Suya crinigera.*	*Suya criniger.*
			Suya fuliginosa.
	Suya atrogularis atrogularis.	*Suya atrigularis.*	*Suya atrogularis.*
	Prinia flaviventris flaviventris.	*Prinia flaviventris.*	*Prinia flaviventris.*
	Prinia socialis socialis.	*Prinia socialis.*	*Prinia socialis.*
	Prinia socialis stewarti.	*Prinia socialis.*	*Prinia stewarti.*
	Prinia sylvatica sylvatica.	*Prinia sylvatica.*	*Drymoipus sylvaticus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Olivaceous Tree-Warbler.	——	——	v. pl. 65.
Green Willow-Warbler.	iv. pls. 88, fig. 8; 171, fig. 5.	——	v. pls. 62, 64.
Large-billed Willow-Warbler.	iv. pl. 86, fig. 9.	——	v. pl. 61.
Dull Green Willow-Warbler.	——	——	v. pl. 61.
Large Crowned Willow-Warbler.	——	——	v. pl. 65.
Blyth's Crowned Willow-Warbler.	——	ii. fig. 349.	v. pls. 64, 65, 66
Allied Flycatcher-Warbler.	iv. pl. 92.	——	v. pl. 66.
Black-browed Fly-catcher-Warbler.	iv. pl. 89.	——	v. pls. 64, 66.
Grey-headed Warbler.	iv. pls. 90, 157, fig. 8.	——	v. pls. 66, 68 ?, 69.
Kashmir Grey-headed Warbler.	——	——	v. pl. 69.
Grey-cheeked Fly-catcher-Warbler.	——	——	v. pl. 69.
Chestnut-headed Fly-catcher-Warbler.	iv. pls. 85, fig. 4; 93.	——	v. pl. 70.
Yellow-bellied Fly-catcher-Warbler.	iv. pl. 91.	——	——
Burmese Yellow-bellied Flycatcher-Warbler.	——	ii. fig. 389.	——
Black-faced Flycatcher-Warbler.	iv. pl. 85, fig. 6.	——	v. pl. 67.
Broad-billed Flycatcher-Warbler.	iv. pl. 94.	——	——
Aberrant Warbler.	iv. pls. 81, 82, 83, 84.	——	——
Strong-footed Bush-Warbler.	iv. pl. 80.	——	——
Pale Bush-Warbler.	——	——	v. pl. 59.
Rufous-capped Bush-Warbler.	iv. pls. 67, fig. 1; 68, 69.	——	v. pl. 60.
Brown Hill-Warbler.	iv. pl. 76, figs. 1, 3.	——	v. pls. 57, 60.
Black-throated Hill-Warbler.	iv. pl. 74.	——	v. pl. 58.
Yellow-bellied Wren-Warbler.	——	i. fig. 142.	——
Ashy Wren-Warbler.	——	——	v. pls. 54, 56.
Stewart's Ashy Wren-Warbler.	——	——	v. pl. 53.
Jungle Wren-Warbler.	- - -	——	v. pls. 55, 56.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Prinia inornata inornata.	*Prinia inornata.*	*Drymoipus inornatus.*
	Prinia inornata burmanica.	*Prinia inornata.*	*Drymoipus inornatus.*
	Prinia inornata jerdoni.	*Prinia jerdoni.*	*Drymoica jerdoni.*
	Family TURDIDÆ.		
	Subfamily Brachypterygin æ.		
	Brachypteryx major major.	*Brachypteryx rufiventris.*	*Kallene rufiventris.*
	Larvivora brunnea.	*Larvivora brunnea.*	*Larvivora cyana.*
	Heteroxenicus nipalensis nipalensis.	*Drymochares nipalensis.*	*Brachypteryx nipalensis.*
	Heteroxenicus cruralis.	*Drymochares cruralis.*	*Brachypteryx cruralis.*
	Hodgsonius phœnicuroides phœnicuroides.	*Hodgsonius phœnicuroides.*	*Hodgsonius phœnicuroides.*
	Subfamily Saxicolin æ.		
	Saxicola caprata bicolor.	*Pratincola caprata.*	*Pratincola caprata.*
	Saxicola caprata atrata.	*Pratincola atrata.*	*Pratincola atrata.*
	Saxicola torquata indica.	*Pratincola maura.*	*Pratincola indica.*
	Oreicola ferrea ferrea.	*Oreicola ferrea.*	*Pratincola ferrea.*
	Œnanthe picata.	*Saxicola picata.*	*Saxicola picata.*
	Œnanthe opistholeuca.	*Saxicola opistholeuca.*	*Saxicola leucuroides.*
	Œnanthe œnanthe œnanthe.	*Saxicola œnanthe.*	*Saxicola œnanthe.*
	Œnanthe deserti atrogularis.	*Saxicola deserti.*	*Saxicola deserti.*
	Cercomela fusca.	*Cercomela fusca.*	*Cercomela fusca.*
	Subfamily Enicurin æ.		
	Enicurus maculatus maculatus.	*Henicurus maculatus.*	*Enicurus maculatus.*
	Enicurus maculatus guttatus.	*Henicurus guttatus.*	*Enicurus maculatus.*
	Enicurus schistaceus.	*Henicurus schistaceus.*	*Enicurus schistaceus.*
	Enicurus immaculatus.	*Henicurus immaculatus.*	*Enicurus immaculatus.*
	Hydrocichla frontalis.	*Hydrocichla frontalis.*	——
	Microcichla scouleri scouleri.	*Microcichla scouleri.*	*Enicurus scouleri.*
			Enicurus nigrifrons.
	Subfamily Phœnicurin æ.		
	Phœnicurus phœnicurus phœnicurus.	*Ruticilla phœnicura.*	*Ruticilla phœnicura.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Indian Wren-Warbler.	iv. pl. 75.	——	v. pl. 55 (2 upper figures).
Burmese Wren-Warbler.	——	ii. fig. 426.	——
Ceylon Wren-Warbler.	——	——	v. pl. 56 ?.
Rufous-bellied Short Wing.	——	——	iii. pl. 69.
Indian Blue Chat.	iii. pl. 99, figs. 4, 5.	——	v. pl. 46.
Nepal Short Wing.	iii. pls. 104, 105, 106 (2 right hand figures).	——	——
White-browed Short Wing.	iii. pl. 106, figs. 1, 2, 3.	——	——
Hodgson's Short Wing.	iii. pls. 109, 110.	——	iii. pl. 70.
Northern Indian Pied Bushchat.	iv. pls. 34, 40, fig. 4.	i. fig. 86.	v. pl. 32.
Southern Indian Pied Bushchat.	——	——	v. pl. 33.
Indian Stonechat.	iv. pl. 35, figs. 1, 2, 5; pls. 37, 38, 39.	i. fig. 345.	v. pl. 34.
Western Dark-grey Bushchat.	iv. pl. 40, figs. 1, 5; pl. 41; pl. 42, nest.	ii. figs. 384 *a*, 429 *b*.	v. pls. 35, 36, 37 39.
Pied Chat.	——	——	v. pl. 38.
Strickland's Chat or Indian White-tailed Stonechat.	iv. pl. 40, figs. 3, 6.	——	v. pl. 40.
Wheatear.	——	——	v. pl. 41.
Gould's Desert Chat.	——	——	v. pls. 40, 41.
Brown Rock Chat.	——	——	v. pl. 39.
Western Spotted Forktail.	iv. pls. 95, 96, fig. 1.	——	vi. pls. 1, 2 (upper figure).
Eastern Spotted Forktail.	——	i. fig. 95.	vi. pl. 2 (lower figure)
Slaty-backed Forktail.	iv. pls. 99, 100.	i. fig. 96.	vi. pl. 3.
Black-backed Forktail.	iv. pl. 98.	——	——
White-crowned Forktail.	iv. pl. 102.	——	——
Little Forktail.	iv. pl. 101.	——	vi. pls. 4, 5.
European Redstart. *Note.*—Very rare, not noted in the F.B.I. 2nd ed.	——	——	v. pl. 42.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Phœnicurus frontalis frontalis.	*Phœnicurus frontalis.*	*Ruticilla frontalis.*	*Ruticilla frontalis.*
	Phœnicurus schisticeps.	*Ruticilla schisticeps.*	*Ruticilla schisticeps.*
	Phœnicurus hodgsoni.	*Ruticilla hodgsoni.*	*Ruticilla hodgsonii.*
	Phœnicurus ochrurus rufiventris.	*Ruticilla rufiventris.*	*Ruticilla rufiventris.*
	Chaimarrhornis leucocephala.	*Chimarrhornis leucocephalus.*	*Chæmorrornis leucocephala.*
	Rhyacornis fuliginosa fuliginosa.	*Rhyacornis fuliginosus.*	*Ruticilla fuliginosa.*
Cyanosylvia svecica svecica correct spelling.	*Cyanosylvia suecica suecica.*	*Cyanecula suecica.*	*Cyanecula suecica.*
	Grandala cœlicolor.	*Grandala cœlicolor.*	*Grandala cœlicolor.*
	Calliope calliope.	*Calliope camtschatkensis.*	*Calliope kamschatkensis.*
	Calliope pectoralis pectoralis.	*Calliope pectoralis.*	*Calliope pectoralis.*
	Ianthia cyanura rufilata.	*Ianthia rufilata.*	*Ianthia cyanura.*
	Ianthia indica indica.	*Ianthia indica.*	*Ianthia superciliaris.*
	Ianthia hyperythra.	*Ianthia hyperythra.*	*Ianthia hyperythra.*
	Adelura cœruleocephala.	*Adelura cœruleicephala.*	*Ruticilla cœruleocephala.*
	Notodela leucura.	*Notodela leucura.*	*Myiomela leucura.*
	Saxicoloides fulicata cambaiensis.	*Thamnobia cambaiensis.*	*Thamnobia cambaiensis.*
	Copsychus saularis saularis.	*Copsychus saularis.*	*Copsychus saularis.*
Kittacincla macroura malabarica.	*Kittacincla macroura indica.*	*Cittocincla macrura.*	*Kittacincla macroura.*
	Subfamily Turdinæ.		
	Turdus merula simillimus.	*Merula simillima.*	*Merula simillima.*
	Turdus merula albocinctus.	*Merula albicincta.*	*Merula albocincta.*
	Turdus boulboul.	*Merula boulboul.*	*Merula boulboul.*
	Turdus castaneus castaneus.	*Merula castanea.*	*Merula castanea.*
	Turdus eunomus.	*Merula fuscata.*	*Planesticus fuscatus.*
	Turdus ruficollis.	*Merula ruficollis.*	*Planesticus ruficollis.*
	Turdus atrogularis.	*Merula atrigularis.*	*Planesticus atrogularis.*
	Turdus unicolor.	*Merula unicolor.*	*Geocichla unicolor.*
	Turdus obscurus obscurus.	*Merula obscura.*	——

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Blue-fronted Redstart.	iv. pl. 48, figs. 3, 4.	xi. pl. 13.	v. pl. 43 (upper figure)
White-throated Redstart.	iv. pl. 46.	——	——
Hodgson's Redstart.	iv. pls. 48, fig. 1; 49, fig. 1.	——	v. pl. 43 (lower figure)
Indian Redstart.	iv. pl. 49, fig. 5.	xi. pl. 14.	v. pl. 43 (middle figures).
White-capped Redstart.	iv. pls. 35, fig. 3; 45, 51.	——	v. pls. 44, 45.
Plumbeous Redstart.	iv. pls. 35, fig. 4; 50.	xi. pl. 15.	v. pl. 44; vi. pl. 3.
Lapland or Red-spotted Bluethroat.	iv. pl. 59.	——	v. pls. 50, 51.
Hodgson's Grandala.	iv. pl. 31.	——	——
Common Ruby Throat.	——	1, fig. 313.	v. pl. 50.
Himalayan Ruby Throat.	iv. pl. 58, figs. 2, 3, 4.	——	——
Red-flanked Bush-Robin.	iv. pl. 53.	——	v. pl. 47.
White-browed Bush-Robin.	iv. pl. 56.	——	v. pl. 49.
Rufous-bellied Bush-Robin or Rusty-throated Blue Woodchat.	iv. pls. 54, 55.	——	v. pls. 46 ♀, 48 ♂
Blue-headed Robin.	iv. pl. 49. fig. 9.	——	——
White-tailed Blue Robin.	iv. pls. 30, 58, fig. 1.	——	v. pl. 34.
Brown-backed Indian Robin.	iv. pls. 32, 33.	1, fig. 88.	v. pl. 32.
Indian Magpie-Robin or Dayal Bird.	iv. pls. 27, 28.	1, fig. 279.	v. pl. 30.
Indian Shama.	iv. pl. 29.	1, fig. 87.	v. pl. 31.
Nilgiri Blackbird.	——	——	iv. pls. 21, 22.
White-collared Blackbird.	iii. pl. 138.	viii, pl. 22.	iv. pl. 25.
Grey-winged Blackbird.	iii. pls. 134, 135, 136, 137.	viii. pl. 15.	iv. pls. 23, 24.
Grey-headed Thrush.	iii. pl. 139.	——	iv. pl. 26.
Dusky Thrush.	iii. pl. 143.	——	——
Red-throated Thrush.	iii. pls. 140, 141, fig. 2.	viii, pl. 16.	——
Black-throated Thrush.	iii. pls. 141, 142.	viii. pl. 17.	iv. pls. 27, 28, 29, 30 ?, 31 ?.
Tickell's Thrush.	iii. pls. 128, figs. 1, 2; 130, figs. 2, 3; 131.	——	iv. pl. 19.
Dark Thrush.	——	i. fig. 344; viii. pl. 18; x. pl. 14.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Geokichla wardi correct spelling.	*Geocichla wardi.*	*Geocichla wardi.*	*Turdulus wardi.*
Geokichla citrina citrina.	*Geocichla citrina citrina.*	*Geocichla citrina.*	*Geocichla citrina.*
Geokichla citrina cyanotis.	*Geocichla citrina cyanotis.*	*Geocichla cyanonotus.*	*Geocichla cyanota.*
Turdus viscivorus bonapartei.	*Arceuthornis viscivorus bonapartei.*	*Turdus viscivorus.*	*Turdus hodgsoni.*
	Oreocincla dauma dauma.	*Oreocincla dauma.*	*Oreocincla dauma.*
	Oreocincla dauma nilgiriensis.	*Oreocincla nilgiriensis.*	*Oreocincla nilgiriensis.*
	Oreocincla mollissima mollissima.	*Oreocincla mollissima.*	*Oreocincla mollissima.*
	Zoothera monticola.	*Zoothera monticola.*	*Zoothera monticola.*
	Zoothera marginata.	*Zoothera marginata.*	——
	Monticola erythrogastra.	*Petrophila erythrogastra.*	*Orocetes erythrogastra.*
	Monticola cinclorhyncha.	*Petrophila cinclorhyncha.*	*Orocetes cinclorhynchus.*
	Monticola solitaria pandoo.	*Petrophila cyanus.*	*Petrocossyphus cyaneus.*
	Monticola solitaria affinis.	*Petrophila cyanus.*	*Petrocossyphus cyaneus.*
	Myiophoneus horsfieldii.	*Myiophoneus horsfieldi.*	*Myiophonus horsfieldii.*
	Myiophoneus temminckii temminckii.	*Myiophoneus temminckii.*	*Myiophonus temminckii.*
	Cochoa purpurea.	*Cochoa purpurea.*	*Cochoa purpurea.*
	Cochoa viridis.	*Cochoa viridis.*	*Cochoa viridis.*
Family PRUNELLIDÆ.			
	Laiscopus collaris nipalensis.	*Accentor nepalensis.*	*Accentor nipalensis.*
	Laiscopus himalayanus.	*Accentor himalayanus.*	*Accentor altaicus.*
	Prunella immaculata.	*Tharrhaleus immaculatus.*	*Accentor immaculatus.*
	Prunella rubeculoides.	*Tharrhaleus rubeculoides.*	*Accentor rubeculoides.*
	Prunella strophiata strophiata.	*Tharrhaleus strophiatus*	*Accentor strophiatus.*
Family CINCLIDÆ.			
	Cinclus pallasii tenuirostris.	*Cinclus asiaticus.*	*Hydrobata asiatica.*
Family TROGLODYTIDÆ.			
	Troglodytes troglodytes nipalensis.	*Anorthura nepalensis.*	*Troglodytes nipalensis.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Pied Ground-Thrush.	iii. pls. 125, fig. i; 132, fig. i.	——	iv. pl. 20.
Orange-headed Ground-Thrush.	iii. pls. 128, fig. 3; 129, nest.; 130, fig. 1.	——	iv. pls. 17, 18.
White-throated Ground-Thrush.	——	viii. pl. 14.	——
Himalayan Mistle-Thrush.	iii. pls. 132, fig. 2; 144, fig. 2.	——	——
Small-billed Mountain-Thrush.	iii. pl. 146, fig. 2.	viii. pl. 20; x. pl. 11.	iv. pls. 34, 35.
Nilgiri Thrush.	——	——	iv. pl. 36.
Plain-backed Mountain-Thrush.	iii. pls. 144, fig. 1; 145.	viii. pl. 19; x. pl. 13.	iv. pls. 32, 33.
Large Brown Thrush.	iii. pls. 118, 119, 120.	——	iv. pl. 9.
Lesser Brown Thrush.	——	i. fig. 311; viii. pl. 10.	——
Chestnut-bellied Rock-Thrush.	iii. pls. 122, 123, 124, nest.; iv. pl. 130, fig. 1.	viii. pl. 12.	iv. pls. 12, 13, 14.
Blue-headed Rock-Thrush.	iii. pls. 125, figs. 3, 4; 127, young.	i. fig. 89; viii. pl. 13.	iv. pls. 14, 15, 16.
Indian Blue Rock-Thrush.	——	——	iv. pl. 11.
Burmese Blue Rock-Thrush.	——	viii. pl. 11.	——
Malabar Whistling-Thrush.	——	——	iv. pl. 1.
Himalayan Whistling-Thrush.	iii. pl. 111, 112, 113.	i. fig. 94; viii. pl. 4.	iv. pls. 2, 3.
Purple Thrush.	iv. pls. 127, 128, 129, 130, fig. 2.	x. pl. 20.	——
Green Thrush.	iv. pl. 131.	i. fig. 150.	vi. pl. 20.
Eastern Alpine Hedge-Sparrow.	iv. pl. 171, figs. 1, 2.	——	——
Altai Hedge-Sparrow.	iv. pl. 172.	——	——
Maroon-backed Hedge-Sparrow.	iv. pls. 170, 171, fig. 3.	——	vi. pl. 56.
Robin Hedge-Sparrow.	iv. pl. 174.	——	——
Rufous-breasted Hedge-Sparrow.	iv. pl. 173, nest.	——	vi. pls. 57, 58.
Indian Brown Dipper.	iii. pl. 117, fig. 1; fig. 2, young.	viii. pl. 9.	iv. pl. 8.
Nepal Wren.	iii. pl. 102; iv. pls. 49, fig. 4; 157, fig. 10.	——	ii. pl. 68.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Spelæornis caudatus.	*Urocichla caudata.*	*Pnoepyga caudata.*
	Pnoepyga squamata squamata.	*Pnoepyga squamata.*	*Pnoepyga squamata.*
	Pnoepyga pusilla pusilla.	*Pnoepyga pusilla.*	*Pnoepyga pusilla.*
	Tesia cyaniventer cyaniventer.	*Tesia cyaniventris.*	*Tesia cyaniventer.*
	Tesia castaneocoronata castaneocoronata.	*Oligura castaneicoronata.*	*Tesia castaneocoronata.*
	Family TIMALIIDÆ.		
	Subfamily TIMALIINÆ.		
	Dryonastes ruficollis.	*Dryonastes ruficollis.*	*Garrulax ruficollis.*
	Dryonastes cærulatus cærulatus.	*Dryonastes cærulatus.*	*Garrulax cærulatus.*
	Dryonastes chinensis leucogenys.	*Dryonastes chinensis.*	——
	Garrulax leucolophus leucolophus.	*Garrulax leucolophus.*	*Garrulax leucolophus.*
	Garrulax leucolophus belangeri.	*Garrulax belangeri*	——
	Garrulax pectoralis pectoralis.	*Garrulax pectoralis*	*Garrulax pectoralis*
	Garrulax pectoralis semitorquata.	*Garrulax pectoralis.*	*Garrulax pectoralis.*
	Garrulax moniliger moniliger.	*Garrulax moniliger.*	*Garrulax moniliger.*
	Garrulax albogularis albogularis.	*Garrulax albigularis.*	*Garrulax albogularis.*
	Garrulax strepitans.	*Garrulax strepitans,*	——
	Ianthocincla ocellata.	*Ianthocincla ocellata.*	*Garrulax ocellatus.*
	Ianthocincla rufogularis rufogularis.	*Ianthocincla rufogularis.*	*Trochalopteron rufogulare.*
Trochalopteron correct spelling.	*Trochalopterum erythrocephalum erythrocephalum.*	*Trochalopterum erythrocephalum.*	*Trochalopteron erythrocephalum.*
	Trochalopterum erythrocephalum chrysopterum.	*Trochalopterum chrysopterum.*	*Trochalopteron chrysopterum.*
	Trochalopterum phœniceum phœniceum.	*Trochalopterum phœniceum.*	*Trochalopteron phœniceum.*
	Trochalopterum subunicolor subunicolor.	*Trochalopterum subunicolor.*	*Trochalopteron subunicolor.*
	Trochalopterum affine affine.	*Trochalopterum affine.*	*Trochalopteron affine.*
	Trochalopterum variegatum variegatum.	*Trochalopterum variegatum.*	*Trochalopteron variegatum.*
	Trochalopterum squamatum.	*Trochalopterum squamatum.*	*Trochalopteron squamatum.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Tailed Wren.	iii. pl. 101.	viii. pl. 2, fig. 2.	iii. pl. 66.
Scaly-breasted Wren.	iii. pls. 97, 98, 99, fig. 3; 100, figs. 1, 4.	viii. pl. 2, fig. 1.	—
Brown Wren.	iii. pl. 100, fig. 5.	—	—
Slaty-bellied Wren.	iii. pls. 96, 100, fig. 2.	viii. pl. 1, fig. 2.	—
Chestnut-headed Wren.	iii. pls. 95, 100, fig. 3.	i. fig. 143; viii. pl. 1, fig. 1.	iii. pls. 66, 67
Rufous-necked Laughing Thrush.	iii. pl. 191, fig. 2.	xi. pl. 3.	—
Grey-sided Laughing Thrush.	—	i. fig. 112.	iv. pls. 58, 59.
Black-throated Laughing Thrush.	—	i. fig. 264.	—
Himalayan White-crested Laughing Thrush.	iii. pls. 174, 175, nest; 176.	—	iv. pl. 57.
Burmese White-crested Laughing Thrush.	—	i. fig. 263.	—
Indian Black-gorgeted Laughing Thrush	iii. pls. 180, 181, fig. 2.	—	iv. pl. 62
Burmese Black-gorgeted Laughing Thrush.	—	i. fig. 265.	
Indian Necklaced Laughing Thrush.	iii. pl. 181, fig. 3, 182	—	—
White-throated Laughing Thrush.	iii. pls. 178, 179.	x pl. 8.	iv. pls. 60, 61.
Tickell's Laughing Thrush.	—	i. fig. 332.	—
White-spotted Laughing Thrush.	iii. pl. 181, fig. 3.	—	iv. pls. 63, 64.
Rufous-chinned Laughing Thrush.	iii. pl. 188	—	iv. pl. 72.
Red-headed Laughing Thrush.	iii. pl. 189.	—	iv. pl. 65.
Shillong Yellow-winged Laughing Thrush.	—	—	iv. pl. 66.
Nepal Crimson-winged Laughing Thrush.	iii. pls. 190, 191, fig. 1.	—	iv. pl. 73.
Plain-coloured Laughing Thrush.	iii. pl. 184.	xi. pl. 4.	iv. pls. 67, 69.
Black-faced Laughing Thrush.	iii. pl. 185, fig. 2.	—	iv. pl. 70.
Eastern Variegated Laughing Thrush.	iii. pl. 185, fig. 1.	xi. pl. 2.	iv. pl. 68.
Blue-winged Laughing Thrush.	iii. pl. 187, fig. 1.	x. pl. 9.	iv. pl. 71.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Trochalopterum cachinnans cachinnans.	*Trochalopterum cachinnans.*	*Trochalopteron cachinnans.*
	Trochalopterum lineatum lineatum.	*Trochalopterum lineatum.*	*Trochalopteron lineatum.*
	Trochalopterum lineatum griseicentior.	*Trochalopterum lineatum.*	*Trochalopteron lineatum.*
	Grammatoptila striata striata.	*Grammatoptila striata.*	*Grammatoptila striata.*
	Turdoides terricolor terricolor.	*Crateropus canorus.*	*Malacocircus terricolor.*
	Turdoides terricolor malabaricus.	*Crateropus canorus.*	*Malacocircus malabaricus.*
	Argya earlii.	*Argya earlii.*	*Chatarrhœa earlei.*
	Argya caudata caudata.	*Argya caudata.*	*Chatarrhœa caudata.*
	Argya malcolmi.	*Argya malcolmi.*	*Malacocircus malcolmi.*
	Argya longirostris.	*Argya longirostris.*	*Pyctorhis longirostris.*
	Pomatorhinus schisticeps schisticeps.	*Pomatorhinus schisticeps.*	*Pomatorhinus schisticeps.*
	Pomatorhinus ferruginosus ferruginosus.	*Pomatorhinus ferruginosus.*	*Pomatorhinus ferruginosus.*
	Pomatorhinus ferruginosus albigularis.	*Pomatorhinus albigularis.*	——
	Pomatorhinus horsfieldi travancoriensis.	*Pomatorhinus horsfieldi.*	*Pomatorhinus horsfieldii.*
	Pomatorhinus ruficollis ruficollis.	*Pomatorhinus ruficollis.*	*Pomatorhinus ruficollis.*
	Pomatorhinus erythrogenys erythrogenys.	*Pomatorhinus erythrogenys.*	*Pomatorhinus erythrogenys.*
	Pomatorhinus hypoleucus hypoleucus.	*Pomatorhinus hypoleucus.*	——
Xiphoramphus correct spelling.	*Xiphiramphus superciliaris.*	*Xiphorhamphus superciliaris.*	*Xiphoramphus superciliaris.*
	Timalia pileata bengalensis.	*Timelia pileata.*	*Timalia pileata.*
	Timalia pileata jerdoni.	*Timelia pileata.*	*Timalia pileata.*
	Dumetia hyperythra.	*Dumetia hyperythra.*	*Dumetia hyperythra.*
	Gampsorhynchus rufulus rufulus.	*Gampsorhynchus rufulus.*	*Gampsorhynchus rufulus.*
	Gampsorhynchus rufulus torquatus.	*Gampsorhynchus torquatus.*	*Gampsorhynchus rufulus.*
	Pyctorhis sinensis sinensis.	*Pyctorhis sinensis.*	*Pyctorhis sinensis.*
	Pellorneum ruficeps mandellii.	*Pellorneum mandellii.*	*Pellorneum ruficeps.*
	Pellorneum ruficeps subochraceum.	*Pellorneum subochraceum.*	——
	Cursonia crispifrons.	*Gypsophila crispifrons.*	——
	Turdinulus brevicaudatus brevicaudatus.	*Corythocichla brevicaudata.*	——

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Nilgiri Laughing Thrush.	——	——	iv. pls. 74, 75.
Nepalese Streaked Laughing Thrush.	iii. pl. 193, figs. 2, 3; pl. 200.	——	——
Simla Streaked Laughing Thrush.	——	——	iv. pl. 76.
Striated Laughing Thrush.	iii. pl. 153.	——	iv. pl. 41.
Bengal Jungle Babbler.	iii. pl. 203; iv. pl. 60, fig. 2.	——	iv. pl. 81.
Southern Jungle Babbler.	——	——	iv. pl. 82.
Striated Babbler.	——	——	iv. pls. 86, 87.
Common Babbler.	——	i. fig. 108.	iv. pls. 84, 85.
Large Grey Babbler.	——	——	iv. pl. 83.
Slender-billed Babbler.	iii. pl. 156.	——	——
Slaty-headed Scimitar Babbler.	iii. pls. 169, 170, fig. 2.	——	iv. pl. 53 (middle figure).
Coral-billed Scimitar Babbler.	iii. pl. 168.	x. pl. 19.	iv. pl. 55.
Blyth's Scimitar Babbler.	——	i. fig. 339.	——
Southern Indian Scimitar Babbler.	——	——	iv. pl. 56.
Nepal Rufous-necked Scimitar Babbler.	iii. pl. 165, figs. 1, 2.	i. fig. 107.	iv. pls. 52, 53 (upper figure).
Rusty-cheeked Scimitar Babbler.	iii. pls. 170, 171 nest; 172, fig. 1.	——	iv. pls. 53 (lower figure), 54.
Arrakan Scimitar Babbler.	——	i. fig. 340.	——
Slender-billed Scimitar Babbler.	iii. pl. 173.	i. fig. 106.	——
Bengal Red-capped Babbler.	iii. pls. 164, 165, fig. 3.	——	——
Burmese Red-capped Babbler.	——	viii. pl. 27, fig. 1.	——
Rufous-bellied Babbler.	——	——	iv. pl. 49.
White-headed Shrike-Babbler.	iii. pl. 154.	——	iv. pl. 42.
Ring-necked Shrike-Babbler.	——	ii. fig. 381.	——
Indian Yellow-eyed Babbler.	iii. pl. 155.	viii. pl. 27, fig. 2.	iv. pls. 43, 44.
Mandelli's Spotted Babbler.	iii. pl. 187, fig. 2.	——	iv. pls. 50, 51.
Malay Spotted Babbler.	——	viii. pl. 26, fig. 1.	——
Lime-rock Babbler.	——	i. fig. 341; ii. fig. 341.	——
Short-tailed Wren-Babbler.	——	ii. fig. 348½; viii. pl. 25, fig. 1.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Rimator malacoptilus.	*Rimator malacoptilus.*	*Rimator malacoptilus.*
Malacocincla abbotti abbotti.	*Malacocincla sepiaria abbotti.*	*Turdinus abbotti.*	*Trichostoma abbotti.*
Thringorhina striolata guttata.	*Thringorhina guttata.*	*Thringorhina guttata.*	——
	Stachyris nigriceps nigriceps.	*Stachyris nigriceps.*	*Stachyris nigriceps.*
	Stachyris nigriceps davisoni.	*Stachyris nigriceps.*	*Stachyris nigriceps.*
	Stachyridopsis ruficeps ruficeps.	*Stachyridopsis ruficeps.*	*Stachyris ruficeps.*
	Stachyridopsis pyrrhops.	*Stachyridopsis pyrrhops.*	*Stachyris pyrrhops.*
	Mixornis rubricapilla rubricapilla.	*Mixornis rubricapillus.*	*Mixornis rubicapillus.*
	Mixornis rubricapilla minor.	*Mixornis rubricapillus.*	*Mixornis rubicapillus.*
	Alcippe nepalensis nepalensis.	*Alcippe nepalensis.*	*Alcippe nipalensis.*
	Alcippe poioicephala poioicephala.	*Alcippe phæocephala.*	*Alcippe poiocephala.*
	Pseudominla cinerea.	*Sittiparus cinereus.*	*Minla cinerea.*
	Pseudominla castaneiceps castaneiceps.	*Sittiparus castaneiceps.*	*Minla castaniceps.*
	Fulvetta vinipecta vinipecta.	*Proparus vinipectus.*	*Proparus vinipectus.*
	Lioparus chrysotis.	*Lioparus chrysæus.*	*Proparus chrysæus.*
Subfamily Sibiinæ.			
	Sibia picaoides picaoides.	*Sibia picaoides.*	*Sibia picaoides.*
	Leioptila capistrata capistrata.	*Lioptila capistrata.*	*Sibia capistrata.*
	Leioptila melanoleuca melanoleuca.	*Lioptila melanoleuca.*	——
	Actinodura egertoni egertoni.	*Actinodura egertoni.*	*Actinodura egertoni.*
	Ixops nipalensis nipalensis.	*Ixops nepalensis.*	*Actinodura nipalensis.*
	Staphidia striata striata.	*Staphidia striata.*	*Ixulus striatus.*
	Siva strigula strigula.	*Siva strigula.*	*Siva strigula.*
	Siva cyanouroptera cyanouroptera.	*Siva cyanuroptera.*	*Siva cyanouroptera.*
	Yuhina gularis gularis.	*Yuhina gularis.*	*Yuhina gularis.*
	Yuhina occipitalis occipitalis.	*Yuhina occipitalis.*	*Yuhina occipitalis.*
	Yuhina nigrimentum nigrimentum.	*Yuhina nigrimentum.*	*Yuhina nigrimentum.*
	Ixulus occipitalis	*Ixulus occipitalis.*	*Ixulus occipitalis.*
	Ixulus flavicollis flavicollis.	*Ixulus flavicollis.*	*Ixulus flavicollis.*
	Erpornis xantholeuca xantholeuca.	*Herpornis xantholeuca.*	*Erpornis xantholeuca.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Long-billed Wren-Babbler.	iii. pl. 103.	viii. pl. 3; x. pl. 18.	——
Abbot's Babbler.	iii. pl. 157.	——	——
Tickell's Spotted Babbler.	——	ii. fig. 383; viii. pl. 25, fig. 2.	——
Black-throated Babbler.	iii. pl. 158, figs. 1, 2.	——	iv. pl. 47.
Malay Grey-throated Babbler.	——	viii. pl. 24, fig. 2.	——
Red-headed Babbler.	iii. pl. 163.	——	iv. pls. 48, 49.
Red-billed Babbler.	iii. pl. 162.	——	iv. pl. 47.
Yellow-breasted Babbler.	iv. pl. 155, figs. 1, 2.	i. fig. 275.	iv. pl. 49.
Burmese Yellow-breasted Babbler.	——	viii. pl. 26, fig. 2.	——
Nepal Babbler.	iii. pls. 159, 160.	——	iv. pl. 45.
Nilgiri Quaker Babbler.	——	——	iv. pl. 46.
Dusky-green Tit-Babbler.	iv. pl. 144.	——	vi. pl. 36.
Chestnut-headed Babbler.	iv. pl. 139, fig. 2.	——	vi. pls. 33, 36.
Hodgson's Fulvetta or Plain Brown Tit-Babbler.	iv. pls. 139, fig. 3, 4; 146.	——	vi. pls. 34, 35.
Golden-breasted Fulvetta or Golden-breasted Tit-Babbler.	iv. pl. 145	i. fig. 127.	vi. pls. 30, 34.
Long-tailed Sibia.	iii. pl. 198.	i. fig. 110; viii. pl. 29.	——
Black-headed Sibia.	iii. pls. 196, 197.	viii. pl. 28.	iv. pl. 80.
Tickell's Sibia.	——	ii. fig. 385; viii. pl. 30.	——
Nepal Bar-Wing.	iii. pl. 194.	i. fig. 111.	iv. pls. 77, 78.
Hoary Bar-Wing.	iii. pl. 195.	——	iv. pls. 77, 78.
Tickell's Staphidia.	——	ii. fig. 387.	vi. pl. 36.
Stripe-throated Siva.	iv. pl. 140, nest.	i. fig. 126.	vi. pls. 31, 32.
Hodgson's Blue-winged Siva.	iv. pl. 141.	i. fig. 129.	vi. pl. 32.
Stripe-throated Yuhina.	iv. pl. 149, fig. 4.	vi. pl. 26.	vi. pl. 39.
Slaty-headed Yuhina.	iv. pls. 149, fig. 6; 152.	——	vi. pl. 39.
Black-chinned Yuhina.	iv. pl. 153.	——	vi. pl. 37.
Chestnut-headed Ixula.	——	i. fig. 130.	——
Yellow-headed Ixulus.	iv. pls. 147, 149, fig. 3.	i. fig. 131.	vi. pls. 37, 38.
White-bellied Herpornis.	iv. pl. 155, fig. 3.	——	vi. pl. 40.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Subfamily Leiotrichinæ.		
Leiothrix correct spelling.	*Liothrix lutea callipyga.*	*Liothrix lutea.*	*Leiothrix luteus.*
	Cutia nipalensis nipalensis.	*Cutia nipalensis.*	*Cutia nipalensis.*
	Pteruthius erythropterus.	*Pteruthius erythropterus.*	*Pteruthius erythropterus.*
	Pteruthius æralatus æralatus.	*Pteruthius æralatus.*	——
	Pteruthius melanotis menalotis.	*Pteruthius melanotis.*	*Allotrius ænobarbus.*
	Pteruthius xanthochloris xanthochloris.	*Pteruthius xanthochloris.*	*Allotrius ænobarbus.*
	Myzornis pyrrhoura.	*Myzornis pyrrhoura.*	*Myzornis pyrrhoura.*
	Hilarocichla rufiventer.	*Hilarocichla rufiventris.*	*Pteruthius rufiventer.*
	Mesia argentauris argentauris.	*Mesia argentauris.*	*Leiothrix argentauris.*
	Minla ignotincta.	*Minla igneitincta.*	*Minla ignotincta.*
	Subfamily Paradoxornithinæ.		
	Conostoma æmodium.	*Conostoma æmodium.*	*Conostoma æmodium.*
	Paradoxornis flavirostris.	*Paradoxornis flavirostris.*	*Paradoxornis flavirostris.*
Suthora unicolor unicolor.	*Suthora unicolor.*	*Suthora unicolor.*	*Heteromorpha unicolor.*
Suthora nipalensis correct spelling.	*Suthora nepalensis.*	*Suthora nepalensis.*	*Suthora nipalensis.*
	Suthora poliotis poliotis.	*Suthora poliotis.*	*Suthora poliotis.*
	Suthora fulvifrons fulvifrons.	*Suthora fulvifrons.*	*Suthora fulvifrons.*
	Suthora ruficeps ruficeps.	*Suthora ruficeps.*	*Chleuasicus ruficeps.*
	Family PYCNONOTIDÆ.		
Aethorhynchus lafresnayei correct spelling.	*Aethorhynchus lafresnayi.*	*Aethorhynchus lafresnayii.*	——
	Ægithina tiphia tiphia.	*Ægithina tiphia.*	*Iora typhia.*
	Chloropsis aurifrons aurifrons.	*Chloropsis aurifrons.*	*Phyllornis aurifrons.*
	Chloropsis aurifrons davidsoni.	*Chloropsis malabarica.*	*Phyllornis malabaricus.*
	Chloropsis hardwickii hardwickii.	*Chloropsis hardwickii.*	*Phyllornis hardwickii.*
	Chloropsis viridis zosterops.	*Chloropsis zosterops.*	——
	Chloropsis jerdoni.	*Chloropsis jerdoni.*	*Phyllornis jerdoni.*
	Criniger tephrogenys flaveolus.	*Criniger flaveolus.*	*Criniger flaveolus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Indian Red-billed Liothrix.	iv. pl. 138, nest.	i. fig. 128.	vi. pl. 27.
Nepal Cutia.	iv. pl. 136.	x. pl. 15.	vi. pls. 25, 26.
Red-winged Shrike-Babbler or Shrike-Tit.	iv. pls. 132, 137, figs. 2, 3.	i. fig. 124.	vi. pls. 21, 22.
Tickell's Shrike-Babbler or Shrike-Tit.	——	i. fig. 334.	——
Chestnut-throated Shrike-Babbler or Shrike-Tit.	iv. pl. 134.	i. fig. 132; xi. pl. 16.	vi. pl. 24.
Green Shrike-Babbler or Shrike-Tit.	iv. pl. 135.	——	vi. pl. 24 (inset figure).
Fire-tailed Myzornis.	iv. pl. 154.	——	——
Rufous-bellied Shrike-Babbler or Shrike-Tit.	iv. pl. 133.	——	vi. pl. 23.
Silver-eared Mesia.	iv. pls. 139, fig. 1; 149, fig. 5.	i. fig. 125.	vi. pl. 28.
Red-tailed Minla.	iv. pl. 149, figs. 7, 8.	——	vi. pl. 29.
Great Parrot-Bill.	iii. pl. 152.	——	iv. pls. 39, 40.
Gould's Parrot-Bill.	iii. pl. 147.	——	iv. pl. 37.
Brown Suthora.	iii. pl. 148.	——	——
Ashy-eared Suthora.	iii. pl. 150, fig. 1.	——	——
Blyth's Suthora.	iii. pls. 150, fig. 3; 151.	——	——
Fulvous-fronted Suthora.	iii. pl. 150, fig. 2.	——	iv. pl. 38.
Red-headed Suthora.	iii. pl. 149.	——	——
Great Iora.	——	vi. pl. 21.	——
Common Iora.	iv. pl. 18.	ii. fig. 414; vi. pl. 20.	v. pls. 17, 18.
Golden-fronted Chloropsis, or Green Bulbul. Leaf Bird.	iv. pl. 15, fig. 2.	vi. pl. 23.	v. pl. 20.
Malabar Chloropsis.	——	——	v. pls. 19, 22 ?.
Orange-bellied Chloropsis.	iv. pls. 15, figs. 1, 3; 17.	vi. pl. 24.	v. pl. 21.
Malachite-shouldered Chloropsis.	——	vi. pl. 25.	——
Jerdon's Chloropsis.	——	i. fig. 156; vi. pl. 22.	——
Indian White-throated Bulbul.	iv. pl. 9.	——	v. pl. 9.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Criniger tephrogenys burmanicus.	*Criniger burmanicus.*	——
	Microscelis psaroides psaroides.	*Hypsipetes psaroides.*	*Hypsipetes psaroides.*
	Microscelis psaroides ganeesa.	*Hypsipetes ganeesa.*	*Hypsipetes ganeesa.*
			Hypsipetes neilgherriensis.
Hemixos correct spelling.	*Hemixus flavala flavala.*	*Hemixus flavala.*	*Hemixos flavala.*
	Hemixus flavala davisoni.	*Hemixus davisoni.*	——
Hemixos mcclellandi correct spelling.	*Hemixus macclellandi macclellandi.*	*Hemixus macclellandi.*	*Hypsipetes McLellandi.*
	Hemixus macclellandi tickelli.	*Hemixus tickelli.*	——
	Alcurus striatus.	*Alcurus striatus.*	*Alcurus striatus.*
	Molpastes hæmorrhous hæmorrhous.	*Molpastes hæmorrhous.*	*Pycnonotus hæmorrhous.*
	Molpastes hæmorrhous nigripileus.	*Molpastes nigripileus.*	——
	Molpastes hæmorrhous bengalensis.	*Molpastes bengalensis.*	*Pycnonotus pygæus.*
	Molpastes leucogenys leucogenys.	*Molpastes leucogenys.*	*Otocompsa leucogenys.*
	Xanthixus flavescens flavescens.	*Xanthixus flavescens.*	——
Otocompsa jocosa jocosa.	*Otocompsa emeria emeria.*	*Otocompsa emeria.*	*Otocompsa jocosa.*
Otocompsa jocosa fuscicaudata.	*Otocompsa emeria fuscicaudata.*	*Otocompsa fuscicaudata.*	*Otocompsa jocosa.*
Otocompsa jocosa erythrotis.	*Otocompsa emeria peguensis.*	*Otocompsa emeria.*	*Otocompsa jocosa.*
	Otocompsa flaviventris flaviventris.	*Otocompsa flaviventris.*	*Rubigula flaviventris.*
	Iole icterica.	*Iole icterica.*	*Criniger ictericus.*
	Iole olivacea cinnamomeoventris.	*Iole virescens.*	——
	Pycnonotus finlaysoni finlaysoni.	*Pycnonotus finlaysoni.*	——
	Pycnonotus plumosus plumosus.	*Pycnonotus plumosus.*	——
	Microtarsus poiocephalus.	*Micropus phæocephalus.*	*Brachypodius poiocephalus.*
	Family CAMPEPHAGIDÆ.		
	Pericrocotus speciosus speciosus.	*Pericrocotus speciosus.*	*Pericrocotus speciosus*
	Pericrocotus speciosus flammeus.	*Pericrocotus flammeus.*	*Pericrocotus flammeus.*
	Pericrocotus brevirostris brevirostris.	*Pericrocotus brevirostris.*	*Pericrocotus brevirostris.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Burmese White-throated Bulbul.	——	ii. fig. 360.	——
Himalayan Black Bulbul.	iv. pls. 1, 2, 3, fig. 2.	——	v. pls. 1, 2.
Southern Indian Black Bulbul.	——	ii. fig. 428.	v. pl. 3.
Himalayan Brown-eared Bulbul.	iv. pls. 4, fig. 2; 6.	i. fig. 152.	v. pl. 5.
Davison's Brown-eared Bulbul.	——	ii. fig. 351.	——
Rufous-bellied Bulbul.	iv. pls. 3, fig. 1; 4, fig. 3.	——	v. pl. 4.
Tickell's Bulbul.	——	ii. fig. 359.	——
Striated Green Bulbul.	——	i. fig. 154.	v. pl. 8.
Ceylon Red-vented Bulbul.	——	——	v. pl. 16.
Tenasserim Red-vented Bulbul.	——	i. fig. 286.	——
Bengal Red-vented Bulbul.	iv. pls. 11, fig 1; 13, 14.	i. fig 155.	v. pls. 14, 15.
White-cheeked Bulbul.	iv. pl. 11, fig. 2.	——	v. pls. 11, 12.
Blyth's Bulbul.	——	ii. fig. 413.	——
Bengal Red-whiskered Bulbul.	iv. pl. 12.	——	v. pl. 18 (left-hand figure).
Southern Red-whiskered Bulbul.	——	——	v. pls. 13, 18 (right hand figure).
Burmese Red-whiskered Bulbul.	——	i. fig. 307.	——
Black-crested Yellow Bulbul.	iv. pl. 4, fig. 1.	i. fig. 288.	v. pl. 10.
Yellow-browed Bulbul.	——	——	v. pls. 6, 7.
Tenasserim Olive Bulbul.	——	ii. fig. 373 *a*.	——
Finlayson's Stripe-throated Bulbul.	——	i. fig. 287.	——
Large Olive Bulbul.	——	ii. fig. 361.	——
Grey-headed Bulbul.	——	——	v. pl. 6.
Indian Scarlet Minivet.	iii. pls. 40 (nest only), 41, 42.	vii. pl. 4 (colour not typical); xi. pl. 17.	iii. pl. 33.
Orange Minivet.	——	——	iii. pls. 32, 34.
Indian Short-billed Minivet.	iii. pls. 43, 44, figs. 1, 3, 4, 5.	vii. pl. 5; xi. pl. 18.	iii. pl. 35.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Pericrocotus solaris solaris.	*Pericrocotus solaris.*	*Pericrocotus solaris.*
	Pericrocotus roseus roseus.	*Pericrocotus roseus.*	*Pericrocotus roseus.*
	Pericrocotus peregrinus peregrinus.	*Pericrocotus peregrinus.*	*Pericrocotus peregrinus.*
	Pericrocotus peregrinus vividus.	*Pericrocotus peregrinus.*	*Pericrocotus peregrinus.*
	Pericrocotus peregrinus malabaricus.	*Pericrocotus peregrinus.*	*Pericrocotus peregrinus.*
	Lalage melaschista melaschista.	*Campophaga melanoschista.*	*Volvocivora meluschistos.*
	Lalage meluschista avensis.	*Campophaga melanoptera.*	*Volvocivora meluschistos.*
	Lalage sykesii.	*Campophaga sykesi.*	*Volvocivora sykesi.*
Coracina macei macei.	*Graucalus macei macei.*	*Graucalus macei.*	*Graucalus macei.*
Coracina macei nipalensis.	*Graucalus macei nipalensis.*	*Graucalus macei.*	*Graucalus macei.*
	Family MUSCICAPIDÆ.		
	Hemichelidon sibirica sibirica.	*Hemichelidon sibirica.*	*Hemichelidon fuliginosus*
	Hemichelidon cinereiceps.	*Hemichelidon ferruginea.*	*Alseonax ferruyineus.*
	Siphia strophiata strophiata	*Siphia strophiata.*	*Siphia strophiata.*
	Siphia parva albicilla.	*Siphia albicilla.*	*Erythrosterna leucura.*
	Cyornis hyperythra hyperythra.	*Cyornis hyperythrus.*	*Siphia superciliaris.*
	Cyornis tricolor tricolor.	*Cyornis leucomelanurus.*	*Siphia leucomelanurus.*
	Cyornis superciliaris superciliaris.	*Cyornis superciliaris.*	*Muscicapula superciliaris.*
	Cyornis melanoleuca melanoleuca.	*Cyornis melanoleucus.*	*Erythrosterna maculata.*
	Cyornis melanoleuca westermanni.	*Cyornis melanoleucus.*	*Erythrosterna maculata.*
	Cyornis sapphira.	*Cyornis sapphira.*	*Muscicapula sapphira.*
	Cyornis rubeculoides rubeculoides.	*Cyornis rubeculoides.*	*Cyornis rubeculoides.*
	Cyornis tickelliæ tickelliæ.	*Cyornis tickellii.*	*Cyornis banyumas* *Cyornis tickelliæ.*
	Cyornis magnirostris.	*Cyornis magnirostris.*	*Cyornis magnirostris.*
Briania hodgsoni hodgsoni.	*Nitidula hodgsoni.*	*Nitidula hodgsoni.*	*Nitidula hodgsoni.*
Stoporala correct spelling.	*Stoparola melanops melanops.*	*Stoparola melanops.*	*Eumyias melanops.*
	Stoparola albicaudata.	*Stoparola albicaudata.*	*Eumyias albicaudata.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Yellow-throated Minivet.	iii. pls. 44, fig. 2; 45.	——	iii. pl. 36.
Rosy Minivet.	iii. pl. 46.	vii. pl. 6.	iii. pl. 37.
Small Minivet.	iii. pl. 47.	——	iii. pl. 37.
Burmese Small Minivet.	——	vii. pl. 7.	——
Malabar Small Minivet.	——	——	iii. pl. 38.
Dark Grey Cuckoo-Shrike.	iii. pls. 35, 36, 37, nest.	x. pl. 7.	iii. pls. 29, 30.
Pale Grey Cuckoo-Shrike.	——	ii. fig. 350 *a*; vii. pl. 3.	——
Black-headed Cuckoo-Shrike.	——	——	iii. pls. 26, 27, 28.
Large Indian Cuckoo-Shrike.	——	vii. pl. 2.	iii. pl. 31.
Large Himalayan Cuckoo-Shrike.	iii. pls. 38, 39.	——	——
Sooty Flycatcher.	——	——	iii. pl. 56.
Ferruginous Flycatcher.	iii. pl. 70.	vii. pls. 30, 32.	iii. pl. 51.
Orange-gorgeted Flycatcher.	——	vii. pl. 32, fig. 1.	iii. pls. 52, 62.
Eastern Red-breasted Flycatcher.	——	ii. fig. 391; vii. pl. 32, figs. 2, 3.	iii. pl. 65.
Rufous-breasted Flycatcher.	iii. pl. 90; iv. pl. 157, fig. 4.	vii. pl. 31, fig. 2.	iii. pl. 64.
Slaty-blue Flycatcher.	iii. pls. 87, 89.	——	iii. pls. 56, 61, 63.
White-browed Blue Flycatcher.	——	——	iii. pls. 57, 63.
Indian Little Pied Flycatcher.	iii. pl. 94.	——	——
Burmese Little Pied Flycatcher.	——	vii. pl. 31, fig. 1.	——
Sapphire-headed Flycatcher.	iii. pl. 77.	vii. pl. 33.	iii. pl. 65.
Blue-throated Flycatcher.	iii. pl. 76, fig. 2.	ii. fig. 434 *a*; vii. pl. 35.	iii. pl. 55.
Tickell's Blue Flycatcher.	——	——	iii. pl. 55.
Large-billed Blue Flycatcher.	——	——	iii. pl. 56.
Pigmy Blue Flycatcher.	iii. pl. 78.	——	iii. pl. 65.
Verditer Flycatcher.	iii. pls. 71, 72, figs. 6, 7, 9; 73, nest.	vii. pl. 34.	iii. pl. 53.
Nilgiri Blue Flycatcher.	——	——	iii. pl. 54.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Anthipes monileger monileger.	*Anthipes monileger.*	*Anthipes monileger.*
	Anthipes monileger submonileger.	*Anthipes submonileger.*	——
	Alseonax latirostris pocensis.	*Alseonax latirostris.*	*Alseonax latirostris.*
	Alseonax ruficaudus.	*Alseonax ruficaudus.*	*Cyornis ruficauda.*
	Ochromela nigrorufa.	*Ochromela nigrirufa.*	*Ochromela nigrorufa.*
	Culicicapa ceylonensis ceylonensis.	*Culicicapa ceylonensis.*	*Cryptolopha cinereocapilla.*
	Niltava grandis grandis.	*Niltava grandis.*	*Niltava grandis.*
	Niltava sundara sundara.	*Niltava sundara.*	*Niltava sundara.*
	Niltava macgrigoriæ.	*Niltava macgrigoriæ.*	*Niltava macgrigoriæ.*
	Terpsiphone paradisi paradisi.	*Terpsiphone paradisi.*	*Tchitrea paradisi.*
	Terpsiphone paradisi affinis.	*Terpsiphone affinis.*	*Tchitrea affinis.*
	Hypothymis azurea styani.	*Hypothymis azurea.*	*Myiagra azurea.*
	Chelidorhynx hypoxanthum.	*Chelidorhynx hypoxanthum.*	*Chelidorhynx hypoxantha.*
	Rhipidura aureola aureola.	*Rhipidura albifrontata.*	*Leucocerca albofrontata.*
	Rhipidura albicollis albicollis.	*Rhipidura albicollis.*	*Leucocerca fuscoventris.*
	Rhipidura pectoralis.	*Rhipidura pectoralis.*	*Leucocerca pectoralis.*
	Family HIRUNDINIDÆ.		
	Delichon urbica whiteleyi.	*Chelidon lagopus.*	——
Delichon nipalensis correct spelling	*Delichon nepalensis.*	*Chelidon nepalensis.*	*Chelidon nipalensis.*
	Riparia paludicola chinensis.	*Cotile sinensis.*	*Cotyle sinensis.*
	Ptyonoprogne rupestris.	*Ptyonoprogne rupestris.*	*Cotyle rupestris.*
	Hirundo rustica rustica.	*Hirundo rustica.*	*Hirundo rustica.*
	Hirundo javanica domicola.	*Hirundo javanica.*	*Hirundo domicola.*
	Hirundo smithii filifera.	*Hirundo smithii.*	*Hirundo filifera.*
	Hirundo daurica striolata.	*Hirundo striolata.*	*Hirundo daurica.*
Hirundo daurica nipalensis correct spelling.	*Hirundo daurica nepalensis.*	*Hirundo nepalensis.*	*Hirundo daurica.*
	Hirundo daurica erythropygia.	*Hirundo erythropygia.*	*Hirundo daurica.*

English Name.	Hodgson.	Tickell.	C. F. Sharp
Hodgson's White-gorgeted Flycatcher.	iii. pls. 83, fig. 2; 86.	——	——
Hume's White-gorgeted Flycatcher.	——	ii. fig. 394.	——
Indian Brown Flycatcher.	iii. pls. 72, fig. 2; 84, fig. 5.	vii. pl. 30, fig. 1.	iii. pl. 50.
Rufous-tailed Flycatcher.	——	——	iii. pl. 56.
Black-and-Orange Flycatcher.	——	——	iii. pl. 52.
Grey-headed Flycatcher.	iii. pl. 68.	vii. pl. 29.	iii. pl. 49.
Large Niltava.	iii. pls. 72, fig. 1; 84, fig. 2; 85.	vii. pl. 38.	iii. pl. 60.
Rufous-bellied Niltava.	iii. pls. 76, fig. 1; 81, fig. 1; 82.	vii. pl. 37; xi. pl. 24.	iii. pl. 58.
Small Niltava.	iii. pl. 83, fig. 1.	vii. pl. 36.	iii. pls. 59, 60.
Indian Paradise Flycatcher.	iii. pls. 63, figs. 1, 2, 3; 64.	vii. pl. 25.	xii. pl. 19.
Burmese Paradise Flycatcher.	——	vii. pl. 26.	——
Northern Indian Black-naped Flycatcher.	——	ii. fig. 350, *b*; vii. pl. 27.	iii. pl. 48.
Yellow-bellied Flycatcher.	iii. pl. 67; iv. pl. 157, fig. 1.	——	iii. pl. 48.
White-browed Fantail-Flycatcher.	iii. pl. 66.	vii. pl. 28, fig. 2.	iii. pl. 47.
White-throated Fantail-Flycatcher.	iii. pl. 65.	vii. pl. 28, fig. 1.	iii. pls. 45, 46, 47.
White-spotted Fantail-Flycatcher.	——	——	iii. pl. 46.
Siberian House Martin.	——	ix. pl. 20.	——
Hodgson's House Martin.	ii. pl. 4.	——	i. pl. 42.
Indian Sand Martin.	ii. pls. 2, fig. 2; 3, figs. 1, 3, young birds.	ix. pl. 19.	i. pl. 38.
Crag Martin.	ii. pl. 3, fig. 2.	——	i. pl. 39.
Common Swallow.	ii. pls. 1; 2, fig. 4.	ix. pl. 15.	i. pl. 33.
Nilgiri House Swallow.	——	ii. fig. 375; ix. pl. 16.	——
Indian Wire-tailed Swallow.	——	ix. pl. 17.	i. pls. 34, 35.
Chinese Striated Swallow.	——	ix. pl. 18.	——
Hodgson's Striated Swallow.	ii. pl. 2, fig. 1.	——	i. pls. 36, 37 (upper figure).
Syke's Striated Swallow.	——	——	i. pl. 37 (lower figure).

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Order EURYLAIMIFORMES.			
Eurylaimus javanicus harterti.	*Eurylaimus javanicus javanicus.*	*Eurylæmus javanicus.*	——
	Corydon sumatranus sumatranus.	*Corydon sumatranus.*	——
	Cymbirhynchus macrorhynchus macrorhynchus.	*Cymborhynchus macrorhynchus.*	——
	Serilophus lunatus lunatus.	*Serilophus lunatus.*	——
	Serilophus rubropygius.	*Serilophus rubripygius.*	*Serilophus rubropygia.*
Psarisomus dalhousiæ dalhousiæ.	*Psarisomus dalhousiæ.*	*Psarisomus dalhousiæ.*	*Psarisomus dalhousiæ.*
Calyptomena viridis continentis.	*Calyptomena viridis.*	*Calyptomena viridis.*	——
Order PICIFORMES.			
Family CAPITONIDÆ.			
	Megalaima virens marshallorum.	*Megalæma marshallorum.*	*Megalaima virens.*
	Thereiceryx zeylanicus caniceps.	*Thereiceryx zeylonicus.*	*Megalaima caniceps.*
	Thereiceryx lineatus hodgsoni.	*Thereiceryx lineatus.*	*Megalaima lineata.*
	Thereiceryx viridis.	*Thereiceryx viridis.*	*Megalaima viridis.*
	Cyanops asiatica asiatica.	*Cyanops asiatica.*	*Cyanops asiatica.*
	Cyanops franklinii franklinii.	*Cyanops franklini.*	*Cyanops franklinii.*
	Cyanops franklinii ramsayi.	*Cyanops ramsayi.*	——
	Xantholæma hæmacephala indica.	*Xantholæma hæmatocephala.*	*Xantholæma indica.*
	Xantholæma hæmacephala lutea.	*Xantholæma hæmatocephala.*	*Xantholæma indica.*
Family INDICATORIDÆ.			
	Indicator xanthonotus.	*Indicator xanthonotus.*	*Indicator xanthonotus.*
Family PICIDÆ.			
	Picus squamatus squamatus.	*Gecinus squamatus.*	*Gecinus squamatus.*
	Picus vittatus myrmecophaneus.	*Gecinus striolatus.*	*Gecinus striolatus.*
	Picus vittatus dehræ.	*Gecinus striolatus.*	*Gecinus striolatus.*
	Picus vittatus viridanus.	*Gecinus viridanus.*	——
	Picus canus barbatus.	*Gecinus occipitalis.*	*Gecinus occipitalis.*
	Picus canus hessei.	*Gecinus occipitalis.*	*Gecinus occipitalis.*
	Picus chlorolophus chlorolophus.	*Gecinus chlorolophus.*	*Gecinus chlorolophus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Horsfield's Broadbill.	——	ix. pl. 10.	——
Dusky Broadbill.	——	ix. pl. 9.	——
Black-and-Red Broadbill.	——	ix. pl. 11.	——
Gould's Broadbill.	——	ix. pl. 13.	——
Hodgson's Broadbill.	ii. pls. 37, 39.	ix. pl. 13.	——
Long-tailed Broadbill.	ii. pl. 37; pl. 38. nest.	ix. pl. 12.	i. pls. 66, 67.
Green Broadbill.	——	ix. pl. 14.	——
Great Himalayan Barbet.	ii. pls. 94, 95, 97.	v. pl. 27.	ii. pl. 32.
Northern Green Barbet.	——	v. pl. 28.	ii. pl. 39.
Assam Lineated Barbet.	ii. pl. 96.	——	ii. pl. 33.
Small Green Barbet.	——	——	ii. pls. 34, 35.
Blue-throated Barbet.	ii. pls. 97, 98, 99.	v. pl. 29.	ii. pl. 36.
Golden-throated Barbet.	ii. pl. 99.	——	ii. pls 34, 37.
Ramsay's Golden-throated Barbet.	——	v. pl. 30.	——
Burmese Crimson-breasted Barbet.	——	v. pl. 31, fig. 2.	——
Indian Crimson-breasted Barbet or Coppersmith.	ii. pl. 101.	v. pl. 31, fig. 1.	ii. pls. 38, 39.
Yellow-backed Honey-Guide.	ii. pl. 93.		
Scaly-bellied Green Woodpecker.	iii. pls. 70, 71, 72.	——	ii. pls. 14, 15, 16.
Little Scaly-bellied Green Woodpecker.	——	——	ii. pls. 13, 17.
Himalayan Scaly-bellied Woodpecker.	ii. pl. 73.	——	——
Burmese Scaly-bellied Woodpecker.	——	v. pl. 17.	——
Indian Black-naped Green Woodpecker.	ii. pls. 74, 75, 76, 77.	——	ii. pls. 18, 19.
Burmese Black-naped Woodpecker.	——	v. pl. 18.	——
Eastern Himalayan Small Yellow-naped Woodpecker.	ii. pls. 72, 80, 81.	v. pl. 20, fig. 1.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Picus chlorolophus simlæ.	*Gecinus chlorolophus.*	*Chrysophlegma chlorolophus.*
	Picus chlorolophus chlorolophoides.	*Gecinus chlorolophus.*	*Chrysophlegma chlorolophus.*
	Picus chlorolophus chlorigaster.	*Gecinus chlorogaster.*	*Chrysophlegma chlorophanes.*
	Chrysophlegma flavinucha flavinucha.	*Chrysophlegma flavinucha.*	*Chrysopholeyma flavinucha.*
	Gecinulus grantia grantia.	*Gecinulus grantia.*	*Gecinulus grantia.*
	Hypopicus hyperythrus hyperythrus.	*Hypopicus hyperythrus.*	*Hypopicus hyperythrus.*
	Dryobates himalayensis himalayensis.	*Dendrocopus himalayensis.*	*Picus himalayanus.*
	Dryobates darjellensis.	*Dendrocopus darjilensis.*	*Picus majoroides.*
Dryobates cathpharius correct spelling.	*Dryobates cathparius cathparius.*	*Dendrocopus cathpharius.*	*Picus cathpharius.*
Dryobates macei westermani.	*Dryobates macei.*	*Dendrocopus macii.*	*Picus macei.*
Dryobates macei astratus.	*Dryobates atratus.*	*Dendrocopus atratus.*	——
	Dryobates auriceps.	*Dendrocopus auriceps.*	*Picus brunneifrons.*
	Leiopicus mahrattensis mahrattensis.	*Liopicus mahrattensis.*	*Picus mahrattensis.*
	Yungipicus hardwickii hardwickii.	*Iyngipicus hardwickii.*	*Yungipicus hardwickii.*
	Yungipicus hardwickii mitchellii.	*Iyngipicus pygmæus.*	*Yungipicus pygmæus.*
	Blythipicus pyrrhotis pyrrhotis.	*Pyrrhopicus pyrrhotis.*	*Venilia pyrrhotis.*
	Miglypies jugularis.	*Miglyptes jugularis.*	——
	Micropternus brachyurus williamsoni.	*Micropternus brachyurus.*	——
	Micropternus brachyurus phaioceps.	*Micropternus phæoceps.*	*Micropternus phaioceps*
	Micropternus brachyurus humei.	*Micropternus phæoceps.*	*Micropternus phaioceps.*
	Micropternus brachyurus gularis.	*Micropternus gularis.*	*Micropternus gularis.*
	Brachypternus benghalensis benghalensis.	*Brachypternus aurantius.*	*Brachypternus aurantius.*
Dinopium shorii.	*Dinopicus shorii.*	*Tiga shorei.*	*Chrysonotus shorei.*
	Chrysocolaptes guttacristatus guttacristatus.	*Chrysocolaptes guttacristatus.*	

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Western Himalayan Small Yellow-naped Woodpecker.	——	——	ii. pl. 22.
Burmese Small Yellow-naped Woodpecker.	——	v. pl. 20, fig. 2.	——
Southern India Small Yellow-naped Woodpecker.	——	——	ii. pl. 23.
Large Yellow-naped Woodpecker.	ii. pls. 78, 79.	v. pl. 19.	ii. pls. 20, 21.
Pale-headed Woodpecker.	ii. pl. 83.	v. pl. 23.	——
Eastern Rufous-bellied Woodpecker.	ii. pl. 67.	——	——
Western Himalayan Pied Woodpecker.	——	——	ii. pl. 1
Darjeeling Pied Woodpecker.	ii. pls. 62, 63.	v. pl. 6.	ii. pls. 2, 3
Himalayan Lesser Pied Woodpecker.	ii. pls. 62, 64.	v. pl. 7.	ii. pl. 4.
Fulvous-breasted Pied Woodpecker.	ii. pl. 67.	——	ii pl. 5.
The Stripe-breasted Pied Woodpecker.	——	v. pl. 8.	——
Brown-fronted Pied Woodpecker.	ii. pls. 65, 90.	——	ii. pl. 6
Southern Yellow-fronted Pied Woodpecker.	ii. pl. 66.	v. pl. 9.	ii. pls. 7 8, 9.
Indian Pigmy Woodpecker.	——	v. pl. 10.	ii. pl. 7.
Kumaun or Himalayan Pigmy Woodpecker.	ii. pl. 65.	——	ii. pl. 10.
Red-eared Bay Woodpecker.	ii. pl. 82.	v. pl. 21.	ii. pl. 24
Black-and-Buff Woodpecker.	——	v. pl. 12.	——
Siam Rufous Woodpecker.	——	v. pl. 22.	——
Northern Rufous Woodpecker.	ii. pl. 84.	——	——
Western Rufous Woodpecker.	——	——	ii. pl. 25.
Southern Rufous Woodpecker.	——	——	ii. pl. 26.
Northern Golden-backed Woodpecker.	ii. pls. 82, 85.	v. pl. 14.	ii. pl. 27.
Himalayan Golden-backed three-toed Woodpecker.	ii. pls. 86, 87, 88.	v. pls. 15, 16.	——
Tickell's Golden-backed Woodpecker.	——	v. pl. 13.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Chrysocolaptes guttacristatus sultaneus.	*Chrysocolaptes guttacristatus.*	*Chrysocolaptes sultaneus.*
	Chrysocolaptes festivus.	*Chrysocolaptes festivus.*	*Chrysocolaptes goensis.*
	Hemicircus canente canente.	*Hemicercus canente.*	*Hemicircus canente.*
	Mulleripicus pulverulentus harterti.	*Hemilophus pulverulentus.*	*Mulleripicus pulverulentus.*
	Picumnus innominatus innominatus.	*Picumnus innominatus.*	*Vivia innominata.*
	Sasia ochracea ochracea.	*Sasia ochracea.*	*Sasia ochracea.*
Jynx torquilla torquilla correct spelling.	*Iynx torquilla torquilla.*	*Iynx torquilla.*	*Yunx torquilla.*

Order COCCYGIFORMES.

Family CUCULIDÆ.

	Cuculus canorus telephonus.	*Cuculus canorus.*	*Cuculus canorus.*
	Cuculus optatus.	*Cuculus saturatus.*	*Cuculus himalayanus.*
	Cuculus poliocephalus poliocephalus.	*Cuculus poliocephalus.*	*Cuculus poliocephalus.*
	Cuculus micropterus micropterus.	*Cuculus micropterus.*	*Cuculus micropterus.* *Cuculus striatus.*
Hierococcyx sparverioides correct spelling.	*Hierococcyx sparveroides.*	*Hierococcyx sparverioides.*	*Hierococcyx sparverioides.*
	Hierococcyx varius.	*Hierococcyx varius.*	*Hierococcyx varius.*
	Hierococcyx fugax nisicolor.	*Hierococcyx nisicolor.*	*Hierococcyx nisicolor.*
	Cacomantis merulinus passerinus.	*Cacomantis passerinus.*	*Polyphasia nigra.*
	Cacomantis merulinus querulus.	*Cacomantis merulinus.*	*Polyphasia tenuirostris.*
	Penthoceryx sonneratii sonneratii.	*Penthoceryx sonnerati.*	*Cuculus sonneratii.*
Chalcites xanthorhynchus xanthorhynchus.	*Chalcites xanthorhynchus.*	*Chrysococcyx xanthorhynchus*	——
	Chalcites maculatus maculatus.	*Chrysococcyx maculatus.*	*Chrysococcyx hodgsoni.*
	Surniculus lugubris dicruroides.	*Surniculus lugubris.*	*Surniculus dicruroides.*
	Clamator jacobinus jacobinus.	*Coccystes jacobinus.*	*Coccystes melanoleucos.*
	Clamator coromandus.	*Coccystes coromandus.*	*Coccystes coromandus.*
Eudynamys correct spelling.	*Eudynamis scolopaceus scolopaceus.*	*Eudynamis honorata.*	*Eudynamys orientalis.*
	Rhopodytes viri virostris.	*Rhopodytes viridirostris.*	*Zanclostomus viridirostris.*
	Rhopodytes tristis tristis.	*Rhopodytes tristis.*	*Zanclostomus tristis.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Hodgson's Golden-backed Woodpecker.	ii. pl. 69.	——	ii. pl. 11.
Black-backed Woodpecker.	——	——	ii. pl. 12.
Heart-spotted Woodpecker	——	v pl. 11.	——
Indian Great Slaty Woodpecker.	——	——	xii. pl. 22.
Himalayan Speckled Piculet.	ii. pl. 90.	v pl. 24.	ii. pls. 6, 29
Indian Rufous Piculet.	ii. pl. 90	v. pl. 25.	——
Wryneck.	ii. pl. 92	v. pl. 26.	ii. pls 30 31
Asiatic Cuckoo.	ii. pl 102.	——	ii. pls 40, 41, 43, 49
Himalayan Cuckoo.	ii. pl. 113.	v. pl. 41.	ii. pls. 42, 45
Small Cuckoo.	——	v pl. 40.; xi. pl. 10.	ii. pls. 46, 49.
Indian Cuckoo.	ii. pls. 106, 107.	x pl. 27.	ii. pls. 47, 48 50
Large Hawk-Cuckoo.	ii. pls. 102, 109, 110.	v. pl. 43	ii pls. 53, 54
Common Hawk-Cuckoo.	——	v. pl. 42.	ii. pls. 51, 52.
Hodgson's Hawk-Cuckoo.	ii. pl. 108.	xi. pl. 7.	——
Indian Plaintive Cuckoo.	ii. pl. 111.	——	ii. pl. 55.
Burmese Plaintive Cuckoo (Rufous-bellied Cuckoo).	——	v. pl. 44.	——
Indian Banded Bay Cuckoo.	ii. pl. 115, young bird.	——	——
Violet Cuckoo.	——	v. pl. 45.	——
Emerald Cuckoo	ii. pl. 115.	——	ii. pl 57, ♀
Indian Drongo-Cuckoo.	ii. pl 113	v. pl. 46.	ii. pl. 56.
Pied Crested Cuckoo.	ii. pl. 116.	v. pl. 38.	ii. pl. 58.
Red-winged Crested Cuckoo.	ii. pl. 117.	v. pl. 39.	ii. pl. 59.
Indian Koel.	ii. pls. 118, 119.	v. pl. 37; xi. pl. 8.	ii. pls. 60 61
Small Green-billed Malkoha.	——	——	ii. pl 62
Large Himalayan Green-billed Malkoha.	ii. pl. 120.	——	xii pl. 27.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Rhopodytes tristis longicaudatus.	*Rhopodytes tristis.*	*Zanclostomus tristis.*
	Rhamphococcyx erythrognathus.	*Rhamphococcyx erythrognathus.*	——
	Taccocua leschenaulti affinis.	*Taccocua leschenaulti.*	*Taccocua sirkee.*
	Taccocua leschenaulti sirkee.	*Taccocua leschenaulti.*	——
	Centropus sinensis sinensis.	*Centropus sinensis.*	*Centropus rufipennis.*
	Centropus sinensis parroti.	*Centropus sinensis.*	*Centropus rufipennis.*
	Centropus bengalensis bengalensis.	*Centropus bengalensis.*	*Centropus viridis.*

Order TROGONIFORMES.

	Pyrotrogon fasciatus malabaricus.	*Harpactes fasciatus.*	*Harpactes fasciatus.*
	Pyrotrogon erythrocephalus erythrocephalus.	*Harpactes erythrocephalus.*	*Harpactes hodgsoni.*
	Pyrotrogon oreskios uniformis.	*Harpactes orescius.*	——

Order CORACIIFORMES.

Family MICROPODIDÆ.

	Micropus melba melba.	*Cypselus melba.*	*Cypselus melba.*
	Micropus affinis affinis.	*Cypselus affinis.*	*Cypselus affinis.*
	Micropus pacificus pacificus.	*Cypselus pacificus.*	*Cypselus leuconyx.*
	Collocalia unicolor unicolor.	*Collocalia fuciphaga.*	*Collocalia nidifica.*
	Collocalia fuciphaga brevirostris.	*Collocalia brevirostris.*	*Collocalia nidifica.*
	Hirundapus caudacutus nudipes.	*Chætura nudipes.*	*Acanthylis nudipes.*
	Hemiprocne coronata.	*Macropteryx coronata.*	*Dendrochelidon coronatus.*
Cypsiurus balasiensis balasiensis correct name.	*Tachornis batasiensis batasiensis.*	*Tachornis batassiensis.*	*Cypselus batassiensis.*

Family CAPRIMULGIDÆ.

Caprimulgus macrurus albonotatus.	*Caprimulgus macrourus albonotatus.*	*Caprimulgus macrurus.*	*Caprimulgus albonotatus.*
Caprimulgus macrurus nipalensis correct spelling.	*Caprimulgus macrourus nipalensis.*	*Caprimulgus macrurus.*	*Caprimulgus macrourus.*
	Caprimulgus indicus indicus.	*Caprimulgus indicus.*	*Caprimulgus indicus.*
	Caprimulgus asiaticus.	*Caprimulgus asiaticus.*	*Caprimulgus asiaticus.*

English Name.	Hodgson.	Tickell	C. F. Sharpe.
Large Malay Green-billed Malkoha.	——	v. pl. 32.	——
Chestnut-breasted Malkoha.	——	v. pl. 33.	——
Bengal Sirkeer Cuckoo.	ii. pls 126, 127.	v. pl 34.	xii. pl. 25.
Punjab Sirkeer Cuckoo	——	——	x. pl. 28.
Common Coucal or Crow Pheasant.	ii. pls. 121, 122, 123, 124	——	xii. pl. 23.
Southern Coucal or Crow Pheasant.	——	v. pl 35	xii. pl. 24.
Lesser Coucal or Crow Pheasant.	ii. pl. 125.	v. pl 36; xi. pl. 9	ii. pl. 63.
Malabar Trogon.	——	ix. pl 7.	——
Red-headed Trogon.	ii. pls. 16, 17, 18	ix. pl. 6.	i. pls. 52, 53.
Robinson's Yellow-breasted Trogan.	——	i fig. 260; ix pl. 8.	——
Alpine Swift.	——	ix. pl. 25.	i. pls. 40, 41.
Common Indian Swift.	ii. pl. 2.	ix. pl. 26.	i. pl. 42.
Large White-rumped Swift.	——	ii. fig. 412; ix pl. 27.	——
Indian Edible-nest Swiftlet.	——	——	i. pl. 43.
Himalayan Swiftlet.	ii. pl. 6.	——	——
White-throated Spine-tail.	ii. pl. 5.	ix. pl. 22.	i. pls. 44, 45.
Indian Crested Swift.	——	ix. pl. 21.	i. pl. 46.
Palm Swift.	——	ii. fig 28.	——
Indian Long-tailed Nightjar.	ii. pls. 10, 11 ?, 13.	ii. fig. 425; ix. pl. 4.	M.P.* 22.
Nepal Long-tailed Nightjar.	ii. pls. 8 ?, 9 ?, 12, 14, 15 ?	——	i. pl. 48.
Indian Jungle Nightjar.	——	ix. pl. 3.	i. pl. 45.
Common Indian Nightjar.	——	——	i. pls. 49, 50.

* M.P. = Mounted Plate.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Caprimulgus monticolus monticolus.	*Caprimulgus monticola.*	*Caprimulgus monticolus.*
	Caprimulgus mahrattensis.	*Caprimulgus mahrattensis.*	*Caprimulgus mahrattensis.*
	Lyncornis cerviniceps cerviniceps.	*Lyncornis cerviniceps.*	——
	Family BUCEROTIDÆ.		
	Dichoceros bicornis bicornis.	*Dichoceros bicornis.*	*Homraius bicornis.*
	Anthracoceros malabaricus malabaricus.	*Anthracoceros albirostris.*	*Hydrocissa albirostris.*
	Aceros nepalensis.	*Aceros nepalensis.*	*Aceros nipalensis.*
	Rhyticeros subruficollis.	*Rhytidoceros subruficollis.*	——
	Lophoceros birostris.	*Lophoceros birostris.*	*Meniceros bicornis.*
	Ptilolæmus tickelli tickelli.	*Ptilolæmus tickelli.*	——
	Family UPUPIDÆ.		
	Upupa epops epops.	*Upupa epops.*	*Upupa epops.*
	Upupa epops orientalis.	*Upupa indica.*	*Upupa nigripennis.*
	Family MEROPIDÆ.		
	Merops orientalis orientalis.	*Merops viridis.*	*Merops viridis.*
	Merops orientalis birmanus.	*Merops viridis.*	*Merops viridis.*
	Merops superciliosus javanicus.	*Merops philippinus.*	*Merops philippensis.*
	Melittophagus erythrocephalus erythrocephalus.	*Melittophagus swinhoii.*	*Merops quinticolor.*
	Bucia athertoni.	*Nyctiornis athertoni.*	*Nyctiornis athertoni.*
	Family CORACIIDÆ.		
	Coracias benghalensis benghalensis.	*Coracias indica.*	*Coracias indica.*
	Coracias benghalensis affinis.	*Coracias affinis.*	*Coracias affinis.*
	Eurystomus orientalis orientalis.	*Eurystomus orientalis.*	*Eurystomus orientalis.*
	Family ALCEDINIDÆ.		
	Ceryle rudis leucomelanura.	*Ceryle varia.*	*Ceryle rudis.*
	Ceryle lugubris guttulata.	*Ceryle lugubris.*	*Ceryle guttata.*
	Alcedo atthis bengalensis.	*Alcedo ispida.*	*Alcedo bengalensis.*
Cyex erithaca erithaca.	*Ceyx tridactylus tridactylus.*	*Ceyx tridactyla.*	*Ceyx tridactyla.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe
Franklin's Nightjar.	——	——	i. pl. 51.
Sykes's Nightjar.	——	ix. pl. 5.	——
Burmese Great-eared Nightjar.	——	ix. pl. 2.	——
Great Hornbill	ii. pls. 40, 41, 42, 43, 51.	ix. pl. 48.	M.P. 23.
Large Indian Pied Hornbill.	——	ix. pl. 49.	——
Rufous-necked Hornbill.	ii. pls. 46, 47, 49, 50, 52.	ix. pl. 52.	——
Blyth's Wreathed Hornbill.	——	ix. pl. 53.	——
Common Grey Hornbill.	ii. pls. 44, 45	ix. pl. 50.	M.P. 24.
Tickell's Hornbill.	——	ix. pl. 51.	——
Hoopoe.	——	vi. pl. 32.	——
Indian Hoopoe.	iii. pl. 24	——	iii. pl. 9.
Common Indian Bee-eater.	ii. pls. 19, 20, 21.	——	i. pl. 55.
Burmese Green Bee-eater.	——	ix. pl. 29.	——
Blue-tailed Bee-eater.	ii. pl. 22.	ix. pl. 31.	i. pl. 56.
Chestnut-headed Bee-eater.	ii. pl. 21.	ix. pl. 30.	i. pls. 54, 55.
Blue-bearded Bee-eater.	ii. pls. 23, 24.	ix. pl. 32.	i. pl. 57.
Indian Roller.	ii. pls. 25, 26.	ix. pl. 33.	M.P. 25 ; i. pl. 58.
Burmese Roller.	——	ix. pl. 34.	——
Broad-billed Roller.	ii. pl. 27.	ix. pl. 35.	——
Indian Pied Kingfisher.	ii. pl. 36.	ix. pl. 46.	i. pls. 63, 65.
Himalayan Pied Kingfisher.	ii. pls. 34, 35, 36	ix. pl. 47.	M.P. 26; i. pl. 64; xii. pl. 38.
Common Indian Kingfisher.	ii. pl. 33	ix. pl. 45.	i. pls. 62, 65.
Indian Three-toed Kingfisher.	ii. pl. 32	ix. pl. 44.	——

Alternative Name	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Ramphalcyon amauroptera	*Pelargopsis amauroptera.*	*Halcyon amauropterus.*
	Ramphalcyon capensis gurial.	*Pelargopsis gurial.*	*Halcyon leucocephalus*
	Ramphalcyon capensis burmanica.	*Pelargopsis leucocephala.*	*Halcyon leucocephalus.*
	Halcyon smyrnensis fusca.	*Halcyon smyrnensis.*	*Halcyon fuscus.*
	Halcyon pileata	*Halcyon pileata*	*Halcyon atricapillus.*
	Entomothera coromanda coromanda.	*Callialcyon lilacina.*	*Halycon coromandelianus.*
	Sauropatis chloris chloris.	*Sauropatis chloris.*	*Todiramphus collaris*
	Carcineutes pulchellus pulchellus.	*Carcineutes pulchellus.*	——
	Family PODARGIDÆ.		
	Batrachostomus javensis hodgsoni.	*Batrachostomus hodgsoni.*	*Otothrix hodgsonii.*
	Batrachostomus moniliger.	*Batrachostomus moniliger.*	*Batrachostomus moniliger.*
	Order PSITTACIFORMES		
Psittacula eupatria nipalensis correct spelling.	*Psittacula eupatria nepalensis.*	*Palæornis nepalensis.*	*Palæornis alexandri*
	Psittacula krameri manillensis.	*Palæornis torquatus.*	*Palæornis torquatus.*
	Psittacula krameri borealis.	*Palæornis torquatus.*	*Palæornis torquatus.*
	Psittacula cyanocephala bengalensis.	*Palæornis rosa.*	*Palæornis rosa.*
	Psittacula schisticeps schisticeps.	*Palæornis schisticeps.*	*Palæornis schisticeps.*
	Psittacula alexandri fasciatus.	*Palæornis fasciatus.*	*Palæornis javanicus.*
	Psittacula columboides.	*Palæornis columboides.*	*Palæornis columboides.*
	Coryllis vernalis vernalis.	*Loriculus vernalis.*	*Loriculus vernalis.*
	Coryllis vernalis rubropygialis.	*Loriculus vernalis.*	*Loriculus vernalis.*
	Order STRIGIFORMES.		
Tyto alba stertens.	*Tyto alba javanica.*	*Strix flammea.*	*Strix javanica.*
Tyto longimembris longimembris.	*Tyto longimembris.*	*Strix candida.*	*Strix candida.*
	Phodilus badius saturatus.	*Photodilus badius.*	*Photodilus badius.*
	Asio otus otus.	*Asio otus.*	*Otus vulgaris.*
	Asio flammeus flammeus.	*Asio accipitrinus.*	*Otus brachyotus.*
	Strix indranee indranee.	*Syrnium indrani.*	*Syrnium indranee.*
	Strix indranee newarensis.	*Syrnium indrani.*	*Syrnium newarense.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Brown-winged Kingfisher.	ii. pl. 31	ix. pl. 38.	——
Brown-headed Stork-billed Kingfisher.	ii. pl. 28.	ix. pl. 37.	i. pl. 59.
Burmese Stork-billed Kingfisher.	——	ix. pl. 36.	——
Indian White-breasted Kingfisher.	ii. pls. 29, 30.	ix. pl. 39.	i. pls. 60, 65
Black-capped Kingfisher.	——	ix. pl. 40.	i. pl. 61.
Indian Ruddy Kingfisher.	——	ix. pl. 41.	——
White-collared Kingfisher.	——	ix. pl. 42.	——
Banded Kingfisher	——	ix pl 43	——
Hodgson's Frogmouth.	ii. pl. 7.	——	——
Ceylon Frogmouth (Wynaad Frogmouth).	——	ix. pl. 1	——
Large Indian Parrakeet.	ii. pl. 53.	v. pl. 1.	xii pl. 21.
Rose-ringed Parrakeet.	——	——	i. pl 68.
Eastern Rose-ringed Parrakeet.	ii. pl. 54.	v. pl. 2	——
Eastern Blossom-headed Parrakeet.	ii. pls 55, 56	v. pl. 3.	i. pl. 69
Himalayan Slaty-headed Parrakeet.	ii. pl 55.	——	i. pl. 70.
Indian Red-breasted Parrakeet.	ii. pls. 55, 57, 59, 60.	v. pl. 4.	i pls. 72, 73.
Blue-winged Parrakeet.	——	——	i. pl. 71.
Indian Lorikeet.	ii. pl 61.	v. pl 5.	——
Malabar Lorikeet.	——	——	i. pl. 74.
Indian Barn-Owl.	i. pls. 158, 159.	iv. pl. 20.	i. pl. 22.
Grass-Owl.	——	iv pl. 21.	xii. pl. 35.
Northern Bay-Owl.	i. pl. 160.	——	——
Long-eared Owl.	i. pl. 165.	——	x. pl 23
Short-eared Owl.	i. pl. 166.	iv. pl 13.	M.P 21
Brown Wood-Owl.	——	iv. pl. 377; iv. pl. 1 ?	—
Himalayan Brown Wood-Owl.	i. pls. 161, 162, 163.	——	x. pl. 22.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Strix nivicola.	*Syrnium nivicola.*	*Syrnium nivicolum.*
	Strix seloputo.	*Syrnium seloputo.*	——
	Strix ocellata.	*Syrnium ocellatum.*	*Syrnium sinense.*
	Ketupa zeylonensis hardwickii.	*Ketupa zeylonensis.*	*Ketupa ceylonensis.*
	Ketupa zeylonensis leschenault.	*Ketupa zeylonensis.*	*Ketupa ceylonensis.*
	Ketupa flavipes.	*Ketupa flavipes.*	*Ketupa flavipes.*
	Ketupa ketupa.	*Ketupa javanensis.*	——
	Bubo bubo bengalensis.	*Bubo bengalensis.*	*Urrua bengalensis.*
	Bubo coromandus coromandus	*Bubo coromandus.*	*Urrua coromanda.*
Bubo nipalensis.	*Huhua nipalensis.*	*Huhua nepalensis.*	*Huhua nipalensis.*
	Otus bakkamœna plumipes.	*Scops bakkamœna*	*Ephialtes lempigi.*
	Otus bakkamœna lettia.	*Scops bakkamœna.*	——
	Otus sunia sunia.	*Scops giu.*	*Ephialtes pennatus.*
	Ninox scutulata lugubris.	*Ninox scutulata.*	*Ninox scutellatus*
Carine brama brama.	*Athene brama brama*	*Athene brama.*	*Athene brama.*
	Glaucidium cuculoides cuculoides.	*Glaucidium cuculoides.*	*Athene cuculoides.*
	Glaucidium radiatum radiatum.	*Glaucidium radiatum.*	*Athene radiata.*
	Glaucidium radiatum malabaricum.	*Glaucidium radiatum.*	*Athene malabarica.*
	Glaucidium brodiei brodiei.	*Glaucidium brodiei.*	*Glaucidium brodiæ*
	Glaucidium brodiei tubiger.	*Glaucidium brodiei.*	*Glaucidium brodiæ*
Order ACCIPITIFORMES.			
	Ægypius monachus.	*Vultur monachus.*	*Vultur monachus.*
	Gyps indicus indicus.	*Gyps indicus.*	*Gyps indicus.*
	Pseudogyps bengalensis.	*Pseudogyps bengalensis.*	*Gyps bengalensis.*
Torgos calvus.	*Sarcogyps calvus.*	*Otogyps calvus.*	*Otogyps calvus.*
	Neophron percnopterus ginginianus.	*Neophron ginginianus.*	*Neophron percnopterus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Himalayan Wood-Owl.	i. pl 164.	iv. pl. 3.	——
Malayan Wood-Owl.	——	v. pl. 2.	——
Mottled Wood-Owl.	——	——	M.P. 21. x. pl. 23.
Northern Brown Fish-Owl.	i. pl. 176.	——	M.P. 21.
Bengal Brown Fish-Owl.	——	iv. pl. 7.	——
Tawny Fish-Owl.	i. pl. 177.	——	——
Malay Fish-Owl (Javan Fish-Owl).	——	iv. pl. 8.	——
Indian Great Horned Owl). (Indian Eagle-Owl).	i pls. 167, 168, 170, 171.	iv. pl. 4.	M.P. 21. x. pl. 24.
Dusky Horned Owl (Coromandel Eagle-Owl).	i. pl. 172.	iv. pl. 5.	M.P. 21. x. pl. 25.
Forest Eagle-Owl (Nepalese Eagle-Owl).	i pls. 173, 174, 175.	iv. pl. 6.	——
Punjab Collared Scops Owl.	——	——	i. pl. 25.
Burmese Collared Scops Owl.	i pls. 180, 181, 184.	ii. pl. 378; iv. pl. 12.	——
Northern Indian Scops Owl.	i. pls. 178, 179.	iv. pls. 9, 10, 11.	i. pls. 23, 24.
Indian Brown Hawk-Owl.	i. pl. 189.	iv. pl. 19.	i. pl. 30.
Spotted Owlet.	i pls. 182, 187.	iv. pl. 14.	i. pl. 27.
Western Himalayan Barred Owlet.	i. pls. 184, 185, 186.	i. fig. 23; iv. pl. 16.	i. pl. 32.
Jungle Owlet.	i. pl. 183.	iv. pl. 15.	i. pls. 26, 27.
Malabar Jungle Owlet.	——	——	i. pl. 31.
Western Collared Pigmy Owlet.	——	——	i. pls. 28, 29.
Eastern Collared Pigmy Owlet.	i. pls. 187, 188.	iv. pls. 17, 18.	——
Cinereous Vulture.	i. pls. 4, 5, 6, 7.	iii. pl. 1.	
Indian Long-billed Vulture.	i. pls. 10, 11 ?	iii. pl. 3.	
Indian White-backed Vulture.	i. pls. 12, 13, 14, 15, 16.	iii. pl. 4.	
Black or Pondicherry Vulture (King Vulture).	i. pls. 8, 9.	iii. pl. 2.	M.P. 1.
Smaller White Scavenger Vulture.	i. pls. 17, 18.	iii. pl. 5	M.P. 2.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Circus cyaneus cyaneus.	*Circus cyaneus.*	*Circus cyaneus.*
	Circus pygargus.	*Circus cineraceus.*	*Circus cineraceus.*
	Circus macrourus.	*Circus macrurus.*	*Circus swainsonii.*
	Circus æruginosus æruginosus.	*Circus æruginosus.*	*Circus æruginosus.*
Circus melanoleucos.	*Circus melanoleucus.*	*Circus melanoleucus.*	*Circus melanoleucos.*
	Astur gentilis schvedowi.	*Astur palumbarius.*	*Astur palumbarius.*
	Astur trivirgatus trivirgatus.	*Lophospizias trivirgatus.*	*Astur (Lophospiza) trivirgatus.*
	Astur trivirgatus rufitinctus.	*Lophospizias trivirgatus.*	*Astur (Lophospiza) trivirgatus.*
	Astur badius dussumieri.	*Astur badius.*	*Micronisus badius.*
	Accipiter nisus melanochistus.	*Accipiter nisus.*	*Accipiter nisus.*
	Accipiter virgatus affinis.	*Accipiter virgatus.*	*Accipter virgatus.*
	Accipiter virgatus besra.	*Accipiter virgatus.*	*Accipiter virgatus.*
Buteo buteo vulpinus.	*Buteo vulpinus.*	*Buteo desertorum.*	*Buteo vulgaris.*
Buteo ferox ferox.	*Buteo rufinus rufinus.*	*Buteo ferox.*	*Buteo cancscens*
	Gypaëtus barbatus hemachal-	*Gypaetus barbatus.*	*Gypaetus barbatus.*
	Aquila chrysaetos daphanea.	*Aquila chrysaëtus.*	*Aquila chrysaetos.*
	Aquila heliaca heliaca.	*Aquila heliaca.*	*Aquila imperialis.*
	Aquila nipalensis nipalensis.	*Aquila bifasciata.*	*Aquila imperialis.* (Jerdon does not distinguish the Imperial from the Steppe Eagle.)
	Aquila rapax vindhiana.	*Aquila vindhiana.*	*Aquila fulvescens.*
	Aquila clanga.	*Aquila maculata.*	*Aquila nævia.*
Hieraaëtus fasciatus fasciatus correct spelling.	*Hieraetus fasciatus fasciatus.*	*Hieraëtus fasciatus.*	*Nisaetus bonelli.*
	Spizaetus nipalensis nipalensis.	*Spizaëtus nepalensis.*	*Limnaetus nipalensis.*
	Spizaëtus cirrhatus cirrhatus.	*Spizaëtus cirrhatus.*	*Limnaetus cristatellus.*
	Spizaëtus cirrhatus limnaëtus	*Spizaëtus limnaëtus.*	*Limnaetus niveus.*
	Circaëtus gallicus.	*Circaëtus gallicus.*	*Circaëtus gallicus.*
	Butastur indicus.	*Butastur indicus.*	——
	Butastur teesa.	*Butastur teesa.*	*Poliornis teesa.*
	Spilornis cheeia cheela.	*Spilornis cheela.*	*Spilornis cheela.*
	Spilornis cheela albidus.	*Spilornis cheela.*	*Spilornis cheela.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Hen Harrier.	i. pls. 128, 129, 130, 131.	——	xii. pls. 55, 57.
Montagu's Harrier.	i. pls. 134, 135.	——	xii. pls. 47, 51, 56.
Pale Harrier.	i. pls. 132, 133.	iii. pl. 39.	M.P. 3, 4; xii. pls. 53, 54 *a*.
Marsh Harrier.	i. pls. 138, 139, 140, 141, 142, 143, 144, 145.	——	xii. pls. 39, 41, 43.
Pied Harrier.	i. pl. 136.	iii. pl. 40.	xii. pls. 45, 49.
Eastern Goshawk.	i. pls. 56, 57, 58, 59.	——	——
Crested Goshawk.	——	——	i. pls. 9, 10.
Northern Crested Goshawk.	i. pls. 60, 61, 62, 63.	iii. pl. 19.	i. pl. 8.
Indian Shikra.	i. pls. 65, 66, 67, 68, 69.	iii. pl. 20.	i. pls. 11, 12, 13, 14.
Indian Sparrow-Hawk.	i. pls. 73, 74.	iii. pl. 21.	i. pls. 15, 16; xii. pl. 34.
Northern Besra Sparrow-Hawk.	i. pl. 64	iii. pl. 22.	i. pls. 19, 20.
Southern Besra Sparrow-Hawk.	——	——	i. pls. 17 ?, 18.
Desert Buzzard (Common Buzzard of Jerdon & F.B.I. 1st Ed.)	——	——	M.P. 5.
Long-legged Buzzard.	i. pls. 115, 117, 118, 119.	iii. pl. 37.	x. pl. 14.
Himalayan Bearded Vulture or Lämmergeyer.	i. pls. 19, 20, 21, 22.	iii. pl. 6.	M.P. 7.
Indian Golden Eagle.	i. pl. 75.	——	——
Imperial Eagle.	i. pls. 77, 79, 80.	iii. pls. 7, 8.	M.P. 8.
Steppe Eagle.	i. pls. 76, 81 ?	——	——
Indian Tawny Eagle.	——	iii. pl. 10.	x. pls. 6, 7.
Greater Spotted Eagle.	i. pl. 82.	iii. pl. 9.	——
Bonelli's Eagle (Mohrangs).	i. pls. 95, 96, 97, 98.	iii. pl. 11.	M.P. 9; x. pls. 9, 10.
Hodgson's Hawk-Eagle.	i. pls. 99, 100, 101.	——	M.P. 11.
Crested Hawk-Eagle.	i. pl. 92.	——	M.P. 12.
Changeable Hawk-Eagle.	i. pls. 90, 91.	iii. pl 12.	x. pl. 12.
Short-toed Eagle.	i. pl. 102.	——	M.P. 13.
Grey-faced Buzzard.	——	——	M.P. 6.
White-eyed Buzzard.	i. pls. 23, 24, 25.	iii. pl. 38.	M.P. 14; x. pl. 15.
Indian Crested Serpent-Eagle.	i. pls. 103, 104, 105, 106.	——	——
Lesser-Crested Serpent-Eagle.	——	iii. pl. 14	x. pl. 11.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Concuma leucorypha.	*Haliaëtus leucoryphus.*	*Haliaëtus leucoryphus.*	*Haliætus fulviventer.*
Cuncuma leucogaster.	*Haliaëtus leucogaster.*	*Haliaetus leucogaster.*	*Haliætus leucogaster.*
	Ichthyophaga humilis plumbeus.	*Polioaëtus humilis.*	——
	Ichthyophaga ichthyaetus ichthyaëtus.	*Polioaëtus ichthyaëtus.*	*Polioætus ichthyætus.*
	Lophotriorchis kieneri.	*Lophotriorchis kieneri.*	*Limnaetus kienierii.*
	Ictinaëtus malayensis perniger.	*Ictinaetus malayensis.*	*Neopus malaiensis.*
	Haliastur indus indus.	*Haliastur indus.*	*Haliastur indus.*
Milvus lineatus lineatus	*Milvus migrans lineatus.*	*Milvus melanotis.*	*Milvus govinda.*
	Milvus migrans govinda.	*Milvus govinda.*	*Milvus govinda.*
	Elanus cœruleus vociferus.	*Elanus cœruleus.*	*Elanus melanopterus.*
	Baza leuphotes leuphotes.	*Baza lophotes.*	*Baza lophotes.*
Pernis cristatus ruficollis.	*Pernis ptilorhynchus ruficollis.*	*Pernis cristatus.*	*Pernis cristata.*
	Microhierax cœrulescens cœrulescens.	*Microhierax eutolmus.*	*Hierax eutolmos.*
	Falco peregrinus calidus.	*Falco peregrinus.*	*Falco peregrinus.*
	Falco peregrinus peregrinator.	*Falco peregrinator.*	*Falco peregrinator.*
	Falco peregrinoides babylonicus.	*Falco barbarus.*	*Falco babylonicus.*
	Falco jugger.	*Falco jugger.*	*Falco jugger.*
	Falco subbuteo subbuteo.	*Falco subbuteo.*	*Hypotriorchis subbuteo*
	Falco severus rufipedoides.	*Falco severus.*	*Hypotriorchis severus*
	Falco cherrug cherrug.	*Falco cherrug.*	*Falco sacer.*
Falco chicquera chicquera correct spelling.	*Falco chiquera chiquera.*	*Æsalon chicquera.*	*Hypotriorchis chicquera.*
Falco (Erythropus) amurensis.	*Erythropus amurensis.*	*Erythropus amurensis.*	*Erythropus vespertinus.*
Falco (Cerchneis) tinnunculus tinnunculus.	*Cerchneis tinnunculus tinnunculus.*	*Tinnunculus alaudarius.*	*Tinnunculus alaudarius.*
Falco (Cerchneis) tinnunculus interstinctus.	*Cerchneis tinnunculus interstinctus.*	*Tinnunculus alaudarius.*	*Tinnunculus alaudarius.*
Falco (Cerchneis) tinnunculus objurgatus.	*Cerchneis tinnunculus objurgatus.*	*Tinnunculus alaudarius.*	*Tinnunculus alaudarius.*
Falco (Cerchneis) naumanni pekinensis.	*Cerchneis naumanni pekinensis.*	*Tinnunculus cenchris.*	*Erythropus cenchris.*
Pandion haliætus haliætus correct spelling.	*Pandion haliaëtus haliaëtus*	*Pandion haliaëtus.*	*Pandion haliætus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Pallas's Fishing Eagle (Ring-tailed Sea Eagle).	i. pl. 108.	iii. pl. 17.	M.P. 15.
White-bellied Sea Eagle.	——	iii. pl. 18.	——
Himalayan Grey-headed Fishing Eagle.	i. pls. 109, 110.	——	——
Large Grey-headed Fishing Eagle.	i. pl. 111.	iii. pl. 16.	x. pl. 13.
Rufous-bellied Hawk-Eagle.	i. pl. 78.	iii. pl. 13.	——
Indian Black Eagle.	i. pl. 88.	——	M.P. 10; x. pl. 8.
Brahminy Kite.	i. pl. 146.	iii. pl. 32.	M.P. 16; xii. pl. 37.
Large Indian Kite.	——	——	x. pl. 16.
Common Pariah Kite.	i. pls. 148, 149, 150.	iii. pl. 33.	x. pls. 17, 18.
Black-winged Kite.	i. pls. 156, 157.	iii. pl. 34.	xii. pls. 36, 56.
Indian Black-crested Baza (Black-crested Kite).	i. pls. 154, 155.	——	——
Indian Crested Honey Buzzard.	i. pls. 151, 152, 153.	ii. fig. 372; iii. pls. 35, 36.	x. pls. 19, 20, 21.
Red-legged Falconet.	i. pl. 55.	iii. pl. 31.	i. pl. 7.
Eastern Peregrine Falcon.	i. pls. 23, 24, 30, 31.	iii. pl. 23.	xii. pl. 69.
Shahin Falcon.	i. pls. 25, 27, 28.	iii. pl. 24.	xii. pls. 65, 67.
Barbary Falcon.	i. pls. 26, 29.	——	——
Laggar Falcon.	i. pl. back of 34.	iii. pl. 25.	M.P. 18; xii. pl. 59.
Hobby.	i. pls 39, 40.	iii. pl. 26.	i. pl. i.
Indian Hobby.	i. pls. 39, 40, 41.	iii. pl. 27.	i. pl. 2; xii. pl. 56.
Cherrug or Saker Falcon.	i. pls. 33, 34.	——	xii. pls. 61, 63.
Red-headed Merlin (Turumti).	i. pls. 42, 43.	iii. pl. 28.	M.P. 17. i. pl. 3.
Eastern Red-legged Falcon.	i. pls. 52, 53.	iii. pl. 29.	——
Kestrel.	i. pls. 44, 46, 47.	iii. pl. 30.	x. pls. 2, 3; pl. 4, fig. 2?
Himalayan Kestrel.	i pl. 45.	——	x. pl. 4, fig. 1.
Indian Kestrel.	——	——	i. pls. 4, 5, 6. [Wrongly named Lesser Kestrel.]
Eastern Lesser Kestrel	i. pls. 51, 52.	——	——
Osprey.	i. pl. 107.	iii. pl. 15.	M.P. 19; i. pl. 21.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Order PELECANIFORMES.		
	Family PHALACROCORACIDÆ.		
Phalacrocorax carbo indicus.	*Phalacrocorax carbo sinensis.*	*Phalacrocorax carbo.*	*Graculus carbo.*
	Phalacrocorax niger.	*Phalacrocorax javanicus.*	*Graculus javanicus.*
	Family ANHINGIDÆ.		
	Anhinga melanogaster.	*Plotus melanogaster.*	*Plotus melanogaster.*
	Family PELECANIDÆ.		
Pelecanus onocrotalus roseus correct spelling.	*Pelecanus onocrocotalus roseus.*	*Pelecanus roseus.*	*Pelecanus javanicus.*
	Pelecanus philippensis.	*Pelecanus philippensis.*	*Pelecanus philippensis.*
	Order PHŒNICOPTERIFORMES.		
	Family PHŒNICOPTERIDÆ.		
	Phœnicopterus ruber antiquorum.	*Phœnicopterus roseus.*	*Phœnicopterus roseus.*
	Order ANSERIFORMES.		
	Cygnus cygnus.	*Cygnus musicus.*	*Cygnus musicus.*
Sarkidiornis melanotos.	*Sarkidiornis melanotus.*	*Sarcidiornis melanonotus.*	*Sarkidiornis melanonotus.*
	Asarcornis scutulatus.	*Ascornis scutulatus.*	*Casarca leucoptera.*
	Rhodonessa caryophyllacea.	*Rhodonessa caryophyllacea.*	*Anas caryophyllacea.*
Nettapus coromandelianus coromandelianus.	*Nettapus coromandelianus.*	*Nettopus coromandelianus.*	*Nettopus coromandelianus.*
	Anser anser.	*Anser ferus.*	*Anser cinereus.*
	Anser indicus.	*Anser indicus.*	*Anser indicus.*
Dendrocygna arcuata arcuata.	*Dendrocygna javanica.*	*Dendrocycna javanica.*	*Dendrocygna awsuree.*
	Tadorna tadorna.	*Tadorna cornuta.*	*Tadorna vulpanser.*
	Casarca ferruginea.	*Casarca rutila.*	*Casarca rutila.*
Anas platyrhynchos platyrhynchos.	*Anas platyrhyncha.*	*Anas boscas.*	*Anas boschas.*
	Anas pœcilorhyncha pœcilorhyncha.	*Anas pœcilorhyncha.*	*Anas pœcilorhyncha.*
Anas angustirostris.	*Marmaronetta angustirostris.*	*Marmaronetta angustirostris.*	——
Anas strepera.	*Chaulelasmus streperus.*	*Chaulelasmus streperus.*	*Chaulelasmus streperus.*
Anas penelope.	*Mareca penelope.*	*Mareca penelope.*	*Mareca penelope*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Indian Large Cormorant.	vi. pls. 193, 194, 195.	i. fig. 228	M.P. 27.
Little Cormorant.	vi. pl. 196.	i. fig. 299.	xii pl. 6.
Indian Darter or Snake-bird.	vi. pl. 197.	i. fig. 229.	M.P. 28.
Eastern White or Rosy Pelican.	vi. pl. 192.	——	
Spotted-billed or Grey Pelican.	vi. pl. 191.	i fig. 227.	M.P 29.
Flamingo.	——	——	M.P 30.
Whooper Swan.	vi. pl. 151	——	——
Nukhta or Comb Duck.	——	i. fig. 301.	M.P. 31 ; xi. pl. 11
White-winged Wood Duck.	——	ii. fig. 400.	——
Pink-headed Duck.	vi. pl. 165.	xi. pl. 27.	——
Cotton Teal.	vi. pl. 154.	i. fig. 302.	xi. pl. 13
Grey Lag-Goose.	vi. pl. 152.	i. fig. 230.	M.P. 32.
Bar-headed Goose.	vi. pl. 153.	i. fig. 231.	M.P. 32 ; xi. pl. 10.
Lesser Whistling Teal.	vi. pls. 155, 157.	i. fig. 303.	xi. pls. 14, 24.
Sheld-Duck.	vi. pls. 157, 158.	——	——
Ruddy Sheld-Duck or Brahminy Duck.	vi. pl. 156.	i. fig. 232.	M.P. 33 ; xi. pl. 12.
Mallard.	vi. pls. 162, 163.	——	M.P. 35 ; xi. pl. 16.
Spotbill or Grey Duck.	vi. pl. 164.	i. fig. 233.	M.P. 34, 37 ; xi. pl. 17
Marbled Duck or Teal.	——	——	xi. pl. 21.
Gadwall.	vi. pl. 166.	i. fig. 235.	M.P. 36 ; xi. pl. 18.
Wigeon.	vi. pls. 169, 170.	i. fig. 236.	M.P. 27, 38 ; xi. pl. 20

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Anas acuta acuta.	*Dafila acuta acuta.*	*Dafila acuta.*	*Dafila acuta.*
	Spatula clypeata.	*Spatula clypeata.*	*Spatula clypeata.*
Anas querquedula.	*Querquedula querquedula.*	*Querquedula circia.*	*Querquedula circia*
Anas crecca.	*Nettion crecca crecca.*	*Nettium crecca.*	*Querquedula crecca.*
	Netta rufina.	*Netta rufina.*	*Branta rufina.*
Nyroca nyroca nyroca.	*Nyroca rufa rufa.*	*Nyroca ferruginea.*	*Aythya nyroca.*
	Nyroca ferina ferina.	*Nyroca ferina.*	*Aythya ferina.*
	Nyroca fuligula fuligula.	*Nyroca fuligula.*	*Fuligula cristata.*
	Mergus merganser orientalis.	*Merganser castor.*	*Mergus castor.*
	(*Mergus merganser americanus.*)	——	——
	Mergellus albellus.	*Mergus albellus.*	*Mergellus albellus.*

Order ARDEIFORMES.

Family ARDEIDÆ.

	Ardea cinera rectirostris.	*Ardea cinerea.*	*Ardea cinerea.*
	Ardea sumatrana sumatrana.	*Ardrea sumatrana.*	*Ardea sumatrana.*
	Ardea purpurea manillensis.	*Ardea manillensis.*	*Ardea purpurea.*
	Egretta alba alba.	*Herodias alba.*	*Herodias alba.*
	Egretta intermedia intermedia.	*Herodias intermedia.*	*Herodias egrettoides*
	Egretta garzetta garzetta.	*Herodias garzetta.*	*Herodias garzetta.*
Demigretta sacra sacra.	*Demiegretta sacra sacra.*	*Lepterodius sacer.*	——
	Nycticorax nycticorax nycticorax.	*Nycticorax griseus.*	*Nycticorax griseus.*
	Butorides striatus javanicus.	*Butorides javanica.*	*Butorides javanica.*
	Ardeola grayii.	*Ardeola grayi.*	*Ardeola leucoptera.*
	Bubulcus ibis coromandus.	*Bubulcus coromandus.*	*Buphus coromandus.*
	Ixobrychus minutus minutus.	*Ardetta minuta.*	*Ardetta minuta.*
	Ixobrychus sinensis sinensis.	*Ardetta sinensis.*	*Ardetta sinensis.*
	Ixobrychus cinnamomeus.	*Ardetta cinnamomea.*	*Ardetta cinnamomea.*
	Dupetor flavicollis flavicollis.	*Dupetor flavicollis.*	*Ardetta flavicollis.*
	Botaurus stellaris stellaris.	*Botaurus stellaris.*	*Botaurus stellaris.*

Family CICONIIDÆ.

	Dissoura episcopa episcopa.	*Dissoura episcopus.*	*Ciconia leucocephala.*
	Ciconia ciconia ciconia.	*Ciconia alba.*	*Ciconia alba.*
	Ciconia nigra.	*Ciconia nigra.*	*Ciconia nigra.*
	Anastomus oscitans.	*Anastomus oscitans.*	*Anastomus oscitans.*
	Xenorhynchus asiaticus asiaticus	*Xenorhynchus asiaticus.*	*Mycteria australis.*
	Leptoptilos dubius.	*Leptoptilus dubius.*	*Leptoptilos argala.*
	Leptoptilos javanicus	*Leptoptilus javanicus.*	*Leptoptilos javanica.*
	Ibis leucocephalus leucocephala.	*Pseudotantalus leucocephalus.*	*Tantalus leucocephalus.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Pintail.	vi. pls. 167, 168.	i. fig. 234.	M.P. 39 ; xi. pl. 19.
Shoveler.	vi. pls. 159, 160, 161.	——	M.P. 36, 37 ; xi. pl. 15
Garganey Teal.	vi. pls. 173, 174.	——	M.P. 37 ; xi. pl. 23.
Common Teal.	vi. pls. 171, 172.	——	M.P. 37, 40 ; xi. pl. 22
Red-crested Pochard.	vi. pls. 175, 176, 177, 188.	i. fig. 237.	M.P. 37, 43.
White-eyed Pochard.	vi. pl. 178.	i. fig. 239.	M.P. 37, 41 ; xi. pl. 26.
Pochard or Dun Bird.	——	——	M.P. 42 ; xi. pl. 25.
Tufted Duck.	vi. pl. 179.	i fig. 238.	M.P. 41, 42 ; xi. pls 27, 30.
Eastern Goosander.	vi. pl. 181.	——	——
American Goosander.	——	——	M.P. 44.
Smew.	——	——	xi. pls. 28, 29.
Eastern Heron.	vi. pls. 108, 109, 110	i. fig. 205.	M.P. 46.
Dusky-grey or Typhon Heron.	vi. pl. 110.	ii. fig. 417.	M.P. 45.
Eastern Purple Heron.	vi. pls. 111, 112.	i. fig. 206.	M.P 47.
Eastern Large Egret.	vi. pls. 105, 113.	——	M.P. 48, 50
Indian Smaller Egret.	——	——	M.P. 49.
Little Egret.	vi. pls. 114, 115, 116, 117, nest ; 118, 119.	——	——
Eastern Reef Heron.	——	ii. fig. 418.	——
Night Heron.	vi. pls. 134, 135, 136, 137, 138, 139, 140.	x. pl. 41.	xii. pl. 3.
Indian Little Green Heron.	vi. pl. 129.	——	ix. pls. 37, 38.
Indian Pond Heron or Paddy Bird.	vi. pls. 125, 126, 127, nest ; 128.	i. fig. 208.	M.P. 51 ; xi. pl 5
Cattle Egret.	vi. pls. 120, 121, 122, 123.	i. fig. 209.	M.P. 50 ; xi pl. 3
Little Bittern.	——	i. fig. 212	——
Yellow Bittern.	——	i. fig. 210.	——
Chestnut Bittern.	vi. pls. 130, 131, 132.	i. fig. 211.	——
Black Bittern.	——	i. fig. 214.	——
Bittern.	vi. pl. 133.	i. fig. 213.	M.P. 52.
White-necked Stork.	vi. pls. 106, 107.	ii. fig. 369.	M.P. 59.
White Stork.	——	——	M.P. 53.
Black Stork.	vi. pls. 103, 104.	——	M.P. 54.
Open-bill or Shell Ibis.	vi. pls. 143, 144.		M.P. 55
Black-necked Stork.	vi. pls. 101, 102.	i. fig. 203.	M.P. 56, 57.
Adjutant.	vi. pls. 98, 99, 100.	i. fig. 204.	——
Smaller Adjutant.	——	i. fig. 300.	M.P. 58.
Painted Stork or Wood Ibis.	vi. pl. 141	i. fig. 201.	M.P. 57, 60.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Family PLEGADIDÆ.		
	Threskiornis melanocephalus.	*Ibis melanocephalus.*	*Threskiornis melanocephalus.*
Inocotis papillosus.	*Pseudibis papillosus.*	*Inocotis papillosus.*	*Geronticus papillosus.*
	Plegadis falcinellus falcinellus.	*Plegadis falcinellus.*	*Falcinellus igneus.*
	Family PLATALEIDÆ.		
	Platalea leucorodia major.	*Platalea leucorodia.*	*Platalea leucorodia.*
	Order BALEARICIFORMES.		
	Family BALEARICIDÆ.		
Megalornis grus lilfordi.	*Grus grus lilfordi.*	*Grus communis.*	*Grus cinerea.*
Megalornis antigone antigone.	*Antigone antigone antigone.*	*Grus antigone.*	*Grus antigone.*
Anthropoïdes virgo correct spelling.	*Anthropoides virgo.*	*Anthropoides virgo.*	*Anthropoides virgo.*
	Order CHARADRIIFORMES.		
	Family OTIDIDÆ.		
	Choriotis nigriceps.	*Eupodotis edwardsi.*	*Eupodotis edwardsii.*
Houbaropsis indica.	*Houbaropsis bengalensis.*	*Sypheotis bengalensis.*	*Sypheotides bengalensis.*
Sypheotides aurita.	*Sypheotides indica.*	*Sypheotis aurita.*	*Sypheotides auritus.*
	Chlamydotis undulata macqueenii.	*Houbara macqueeni.*	*Houbara macqueenii.*
	Family BURHINIDÆ.		
	Burhinus œdicnemus indicus.	*Œdicnemus scolopax.*	*Œdicnemus crepitans.*
	Esacus recurvirostris.	*Esacus recurvirostris.*	*Esacus recurvirostris.*
	Family SCOLOPACIDÆ.		
	Tringa totanus totanus.	*Totanus calidris.*	*Totanus calidris.*
	Tringa erythropus.	*Totanus fuscus.*	*Totanus fuscus.*
Tringa ocrophus correct spelling.	*Tringa ochrophus.*	*Totanus ochropus.*	*Actitis ochropus.*
	Tringa glareola.	*Totanus glareola.*	*Actitis glareola.*
	Tringa hypoleucos,	*Totanus hypoleucus.*	*Actitis hypoleucos.*
	Tringa stagnatilis.	*Totanus stagnatilis.*	*Totanus stagnatalis.*
Tringa nebularia	*Glottis nebularia.*	*Totanus glottis.*	*Totanus glottis.*
	Limosa limosa limosa.	*Limosa belgica.*	*Limosa ægocephala.*
	Numenius arquata lineatus.	*Numenius arquata.*	*Numenius arquata.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
White Ibis.	vi. pls. 145, 146, 147.	——	M.P. 61 ; xi pl. 6.
Indian Black Ibis.	vi. pl. 148.	——	M P. 62 ; xi pl. 9.
Glossy Ibis.	vi. pls. 149, 150.	——	——
Indian Spoonbill.	vi. pl. 142.	i. fig. 202.	M.P. 63.
Eastern Common Crane.	vi. pl. 30.	i fig 199.	M.P. 64.
Indian Sarus Crane.	vi. pl. 28.	i. fig 198.	M.P. 65, 66.
Demoiselle Crane.	vi. pl. 29.	——	M.P. 67. x pl. 45.
Great Indian Bustard.	vi. pl. 1.	——	
Bengal Florican.	vi. pls. 3, 4, 5, 6, 8 9.	——	M.P. 69.
Lesser Florican or Likh.	vi. pls. 2, 7, 10.	——	x. pl. 44.
Macqueen's Bustard.	——	——	M.P. 68.
Indian Stone Curlew.	vi. pl. 26.	——	xii. pl. 11.
Great Stone Curlew.	vi. pl. 25.	ii. fig. 410.	xi. pl. 4.
Redshank.	vi. pls. 76, 77.	i. fig. 191 ; x. pl. 39.	ix. pls. 31, 32, 33.
Spotted or Dusky Redshank.	vi. pl. 75.	——	——
Green Sandpiper.	vi. pls. 67, 68, 70.	i. fig. 192.	ix. pl. 26.
Wood Sandpiper.	vi. pls. 65, 66.	ii. fig. 365.	ix. pl. 25.
Common Sandpiper.	vi. pls. 69, 70.	i. fig. 193.	ix. pl. 27.
Marsh Sandpiper or Little Greenshank.	——	——	ix. pl. 30.
Greenshank.	vi. pls. 71, 72, 73, 74.	——	ix. pls. 28, 29.
Black-tailed Godivit.	vi. pl. 50.	——	xi. pls. 7, 8 ; xii. pl. 9.
Eastern Curlew.	vi. pls. 51, 52, 53, 54.	i. fig. 194.	xii. pl. 7.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Numenius phæopus variegatus.	*Numenius phæopus.*	*Numenius phæopus.*
Calidris minuta minuta.	*Erolia minuta minuta.*	*Tringa minuta.*	*Tringa minuta.*
Calidris temminckii.	*Erolia temminckii.*	*Tringa temminckii.*	*Tringa temminckii.*
Calidris alpina alpina.	*Erolia alpina alpina.*	*Tringa alpina.*	*Tringa cinclus.*
	Philomachus pugnax.	*Pavoncella pugnax.*	*Philomachus pugnax.*
	Scolopax rusticola rusticola.	*Scolopax rusticula.*	*Scolopax rusticola*
	Capella gallinago gallinago.	*Gallinago cœlestis.*	*Gallinago scolopacinus*
	Capella stenura.	*Gallinago stenura.*	*Gallinago stenura.*
	Capella nemoricola.	*Gallinago nemoricola.*	*Gallinago nemoricola*
	Capella solitaria.	*Gallinago solitaria.*	*Gallinago solitaria.*
	Lymnocryptes minima	*Gallinago gallinula.*	*Gallinago gallinula.*
	Rostratula benghalensis benghalensis.	*Rostratula capensis.*	*Rhynchæa bengalensis.*

Family CHARADRIIDÆ.

	Squatarola squatarola hypomela.	*Squatarola helvetica.*	*Squatarola helvetica.*
	Pluvialis dominicus fulvus.	*Charadrius fulvus.*	*Charadrius longipes.*
	Charadrius dubius jerdoni.	*Ægialitis dubia.*	*Ægialitis philippensis.*
Charadrius alexandrinus seebohmi.	*Leucopolius alexandrinus seebohmi.*	*Ægialitis alexandrina.*	*Ægialitis cantianus*
Cirrepidesmus mongolus atrifrons correct spelling.	*Cirrepedesmus mongolus atrifrons.*	*Ægialitis mongolica.*	*Ægialitis pyrrothorax.*
	Vanellus vanellus.	*Vanellus vulgaris.*	*Vanellus cristatus.*
	Chettusia gregaria	*Chettusia gregaria.*	*Chettusia gregaria.*
Vanellochettusia leucura.	*Chettusia leucura.*	*Chettusia leucura.*	*Chettusia leucura.*
	Microsarcops cinereus.	*Microsarcops cinereus.*	*Chettusia inornata.*
	Lobivanellus indicus indicus.	*Sarcogrammus indicus.*	*Lobivanellus goensis.*
	Lobipluvia malabarica.	*Sarciophorus malabaricus.*	*Sarciophorus bilobus.*
	Hoplopterus ventralis.	*Hoplopterus ventralis.*	*Hoplopterus ventralis.*
	Hæmatopus ostralegus ostralegus.	*Hæmatopus ostralegus.*	*Hæmatopus ostralegus.*
	Himantops himantopus himantopus.	*Himantopus candidus.*	*Himantopus candidus.*
Recurvirostra avosetta avosetta correct spelling.	*Recurvirostra avocetta avocetta.*	*Recurvirostra avocetta.*	*Recurvirostra avocetta.*
	Ibidorhyncha struthersii.	*Ibidorhynchus struthersi.*	*Ibidorhynchus struthersii.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Eastern Whimbrel.	vi. pl. 55.	i. fig. 195.	——
Little Stint.	vi. pl. 63.	——	——
Temminck's Stint.	vi. pl. 64.	ii. fig. 411.	M.P. 41.
Dunlin.	vi. pl. 62.	——	——
Ruff.	vi. pls. 58, 59, 60, 61.	——	ix. pls. 23, 24.
Woodcock.	vi. pls. 31, 33.	x. pl. 38.	M.P. 70; ix. pls. 14. 15. x. pl. 46.
Common or Fantail Snipe.	vi. pls. 44, 45, 46.	——	ix. pls. 16, 17, 18.
Pintail Snipe.	vi. pls. 42, 43.	xi. pl. 22.	——
Wood Snipe..	vi. pls. 34, 35, 36, 37.	——	xii. pl. 28.
Solitary Snipe.	vi pls. 32. 38, 39, 40, 41.	——	——
Jack Snipe.	vi. pl. 47.	i. fig. 196.	ix. pls. 17, 19, 20.
Painted Snipe.	vi. pls. 48, 49.	——	ix. pls. 20, 21, 22.
Grey Plover.	vi. pl. 15.	——	——
Eastern Golden Plover.	vi. pls. 16, 17.	ii. fig. 402.	——
Jerdon's Little Ringed Plover.	vi. pl. 64.	ii. fig. 409.	ix. pls. 5, 6.
Indian Kentish Plover	vi. pl. 18.	——	ix. pls. 3, 4 and loose plate.
Pamirs Lesser Sand-Plover.	vi. pls. 18, 19.	——	——
Lapwing or Green Plover.	vi. pl. 20.	——	ix. pl. 7.
Sociable Lapwing.	——	——	ix. pls. 8, 9.
White-tailed Lapwing.	——	——	ix. pl. 10.
Grey-headed Lapwing.	——	i. fig 200.	——
Red-wattled Lapwing.	vi. pls. 21, 22.	i. fig. 189.	ix. pl. 11; xii. pl. 10.
Yellow-wattled Lapwing.	vi. pl. 23.	——	ix. pl. 12; xii. pl. 32.
Indian Spur-winged Plover.	vi. pl. 24.	——	xi. pl. 13 and loose plate.
Oyster-catcher.	vi. pl. 27.	——	——
Stilt.	vi. pls. 78, 79.	——	xi. pl. 8.
Avocet.	vi. pl. 80.	x. pl. 40.	——
Ibis-Bill.	vi. pl. 56.	——	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Family JACANIDÆ.		
	Metopidius indicus.	*Metopidius indicus.*	*Metopidius indicus.*
	Hydrophasianus chirurgus.	*Hydrophasianus chirurgus.*	*Hydrophasianus chirurgus.*
	Family GLAREOLIDÆ.		
	Glareola maldivarum maldivarum.	*Glareola orientalis.*	*Glareola orientalis*
Galachrysia lactea.	*Glareola lactea.*	*Glareola lactea.*	*Glareola lactea.*
	Family CURSORIIDÆ.		
	Cursorius coromandelicus.	*Cursorius coromandelicus.*	*Cursorius coromandelicus.*
	Order LARIFORMES.		
	Family STERCORARIIDÆ.		
	Stercorarius pomarinus pomarinus.	*Stercorarius pomatorhinus.*	*Lestris pomarinus.*
	Family LARIDÆ.		
	Larus ichtyaetus.	*Larus ichthyaetus.*	*Kroikocephalus ichthyætus.*
Larus ridibundus ridibundus.	*Larus ridibundus.*	*Larus ridibundus.*	*Xema ridibunda.*
	Larus brunnicephalus.	*Larus brunnicephalus.*	*Xema brunnicephala.*
	Chlidonias leucopareia indica.	*Hydrochelidon hybrida.*	*Hydrochelidon indica.*
	Hydroprogne caspia caspia.	*Hydroprogne caspia.*	*Sylochelidon caspius*
	Gelochelidon nilotica nilotica.	*Sterna anglica.*	*Gelochelidon anglicus.*
	Sterna aurantia.	*Sterna seena.*	*Seena aurantia.*
	Sterna melanogaster.	*Sterna melanogaster.*	*Sterna javanica.*
	Sterna albifrons pusilla.	*Sterna minuta.*	*Sternula minuta.*
	Sterna sumatrana sumatrana.	*Sterna melanauchen.*	*Onychoprion melanauchen.*
	Sterna fuscata infuscata.	*Sterna fuliginosa.*	——
	Family RHYNCOPIDÆ.		
	Rhyncops albicollis.	*Rhyncops albicollis.*	*Rhyncops albicollis.*
	Order PODICIPIDIFORMES.		
	Family PODICIPIDÆ.		
	Podiceps cristatus cristatus.	*Podicipes cristatus.*	*Podiceps cristatus.*
	Podiceps ruficollis capensis.	*Podicipes albipennis.*	*Podiceps philippensis.*

English Name.	Hodgson.	Tickell.	C. F. Sharpe
Bronze-winged Jacana.	vi. pls. 81, 82, 83.	i. fig. 197.	xii. pl. 5.
Pheasant-tailed Jacana.	vi. pl. 84.	——	xi. pl. 1
Large Indian Pratincole or Swallow Plover.	vi pl. 12.	i. fig. 295.	——
Small Indian Pratincole or Swallow Plover.	vi. pls. 13, 14.	i. fig. 296.	ix. loose plate
Indian Courser.	vi. pl. 11.	——	xii. pl. 52.
Pomatorhine Skua.	——	ii. fig. 399.	——
Great Black-headed Gull.	——	i. fig. 220.	xi. pls. 31, 33.
Black-headed Gull.	vi. pls. 184, 185.	——	——
Brown-headed Gull.	vi. pl. 186.	i. fig. 221.	ix. pl. 41.
Indian Whiskered Tern.	——	——	ix. pl 42.
Caspian Tern.	——	i. fig. 223 ; x. pl 44.	xii. pl 2
Gull-billed Tern.	——	i. fig. 224.	xi. pl. 34.
Indian River Tern.	vi. pls. 187, 188.	i. fig. 298.	——
Black-bellied Tern.	vii. pl. 189.	i. fig. 222.	ix pl. 44 ; xii. pl. 2.
River Little Tern.	——	i. fig. 225.	——
Black-naped Tern.	——	i fig. 226.	——
Indian Sooty Tern.	——	ii. fig. 419 ?	——
Indian Skimmer.	vi. pl. 190	i fig. 297.	xi. pl. 34.
Great-crested Grebe.	vi. pl 182.	——	M.P. 37. xi. pl. 32 ; xii. pl 1.
Indian Little Grebe or Dabchick.	vi. p 183	i. fig. 240.	ix. pls. 39, 40

Alternative Name.		Id.	Jerdon.
Order RALLIFORMES.			
Family RALLIDÆ.			
	Rallus aquaticus indicus	*Rallus indicus.*	*Rallus indicus.*
	Porzana pusilla pusilla.	*Porzana pusilla.*	*Porzana pygmæa.*
	Rallina superciliaris superciliaris	*Rallina superciliaris.*	*Porzana ceylonica.*
	Amaurornis fuscus fuscus.	*Amaurornis fuscus.*	*Porzana fusca.*
	Amaurornis akool akool.	*Amaurornis akool.*	*Porzana akool.*
	Amaurornis phœnicurus phœnicurus	*Amaurornis phœnicurus.*	*Gallinula phœnicura.*
	Gallinula chloropus indicus.	*Gallinula chloropus.*	*Gallinula chloropus.*
	Gallicrex cinerea.	*Gallicrex cinerea.*	*Gallicrex cristatus.*
	Porphyrio poliocephalus poliocephalus.	*Porphyrio poliocephalus.*	*Porphyrio poliocephalus.*
	Fulica atra atra.	*Fulica atra.*	*Fulica atra.*
Family HELIORNITHIDÆ.			
	Heliopais personata.	*Heliopais personata.*	—
Order COLUMBIFORMES.			
Family COLUMBIDÆ.			
	Sphenocercus apicaudus apicaudus.	*Sphenocercus apicauda.*	*Sphenocercus apicaudus.*
	Sphenocercus sphenurus sphenurus	*Sphenocercus sphenurus.*	*Sphenocercus sphenurus.*
	Crocopus phœnicopterus phœnicopterus.	*Crocopus phœnicopterus.*	*Crocopus phœnicopterus.*
	Crocopus phœnicopterus viridifrons.	*Crocopus phœnicopterus.*	*Crocopus phœnicopterus.*
Dendrophassa correct spelling.	*Dendrophasa bicincta bicincta.*	*Osmotreron bicincta.*	*Osmotreron bicincta.*
	Dendrophasa pompadora phayrei.	*Osmotreron phayrei.*	*Osmotreron phayrei.*
	Dendrophasa pompadora affinis.	*Osmotreron affinis.*	*Osmotreron malabarica.*
	Treron curvirostra nipalensis.	*Treron nepalensis.*	*Treron nipalensis.*
	Ducula badia insignis.	*Ducula insignis.*	*Carpophaga insignis.*
	Muscadivora ænea sylvatica.	*Carpophaga ænea.*	*Carpophaga sylvatica.*
	Columba leuconota leuconota.	*Columba leuconota.*	*Columba leuconota.*
	Columba livia intermedia.	*Columba intermedia.*	*Columba intermedia.*
	Columba ænas eversmanni.	*Columba eversmanni.*	*Palumbœna eversmanni.*

	Hodgson.	Tickell.	C. F. Sharpe.
Indian Water Rail.	vi pl. 97.	i. fig. 218.	—
Pigmy or Baillon's Crake.	vi. pl. 94.	—	ix. pl. 36.
Banded Crake.	vi. pl. 96.	—	—
Ruddy Crake	vi. pl. 95.	i. fig. 219.	—
Brown Crake.	vi. pl. 93.	—	—
White-breasted Water Hen or Gallinule.	vi. pl. 92.	i. fig. 217.	ix. pl. 35; xii pl. 2 *a*
Indian Moorhen or Waterhen.	vi. pls. 88, 89, 90, 91.	i. fig. 216.	ix. pl. 34.
Kora or Water Cock.	—	ii. fig. 370.	—
Indian Purple Moorhen or Coot.	vi. pl. 85.	i. fig. 215.	xi. pl. 2.
Coot.	vi. pls. 86, 87.	—	xi. pl. 2.
Masked Finfoot.	—	ii. fig. 398.	
Pin-tailed Green Pigeon.	v. pl. 62.	—	viii. pl. 5.
Wedge-tailed Green Pigeon or Kokla.	v. pls 56, 57, 58, 59, 60, 61.	i. fig. 172.	viii. pl. 4.
Bengal Green Pigeon	v. pls 52, 53, 54.	i. fig. 170.	viii. pl. 1.
Burmese Green Pigeon.	—	ii. fig. 433.	—
Indian Orange-breasted Green Pigeon.	v. pl. 55.	—	viii. pl. 2.
Ashy-headed Green Pigeon.	—	i. fig. 291.	—
Grey-fronted Green Pigeon.	—	·	viii. pl. 3, ♀.
Thick-billed Green Pigeon.	v. pls 49, 50, 51.	i. fig. 290 · ii. fig. 361 *a*.	—
Hodgson's Imperial Pigeon.	v. pl. 63.	i. fig. 173.	—
Indian Green Imperial Pigeon.	—	i. fig. 292.	—
Snow Pigeon.	v. pl 69.	—	—
Indian Blue Rock Pigeon.	—	i. fig. 175.	viii. pl. 6.
Eastern or Indian Stock Dove.	—	—	viii. pl. 18; xii. pl. 34.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Columba palumbus casiotis.	*Palumbus casiotis.*	*Palumbus casiotis.*
	Columba pulchricollis.	*Alsocomus pulchricollis.*	*Palumbus pulchricollis.*
	Columba elphinstonii.	*Alsocomus elphinstonii.*	*Palumbus elphinstonei*
Columba puniceus.	*Alsocomus puniceus.*	*Alsocomus puniceus.*	*Alsocomus puniceus.*
Columba hodgsonii.	*Dendrotreron hodgsonii.*	*Dendrotreron hodgsoni.*	*Alsocomus hodgsonii.*
	Macropygia unchall tusalia.	*Macropygia tusalia.*	*Macropygia tusalia.*
	Streptopelia orientalis ferrago.	*Turtur ferrago.*	*Turtur meena.*
Spilopelia chinensis suratensis.	*Streptopelia chinensis suratensis.*	*Turtur suratensis.*	*Turtur suratensis.*
Stigmatopelia senegalensis cambayensis correct spelling.	*Streptopelia senegalensis cambaiensis.*	*Turtur cambayensis.*	*Turtur cambayensis*
	Streptopelia decaocto decaocto.	*Turtur risorius.*	*Turtur risoria.*
	Œnopopelia tranquebarica tranquebarica.	*Œnopopelia tranquebarica.*	*Turtur humilis.*
	Chalcophaps indica indica.	*Chalcophaps indica.*	*Chalcophaps indicus*
	Calœnas nicobarica nicobarica.	*Calœnas nicobarica.*	——

Order TURNICIFORMES.

Family TURNICIDÆ.

	Turnix suscitator taijoor.	*Turnix pugnax.*	*Turnix taigoor*
	Turnix dussumieri.	*Turnix dussumieri.*	*Turnix sykesii*
	Turnix maculatus tanki.	*Turnix tanki.*	*Turnix dussumieri.*

Order PTEROCLETIFORMES.

Family PTEROCLETIDÆ.

Pterocles fasciatus.	*Pterocles indicus.*	*Pterocles fasciatus.*	*Pterocles fasciatus.*
	Pterocles orientalis.	*Pterocles arenarius.*	*Pterocles arenarius.*
Pterocles senegalensis erlangeri.	*Pterocles exustus erlangeri.*	*Pterocles exustus.*	*Pterocles exustus.*

Order GALLIFORMES.

Family PHASIANIDÆ.

Subfamily PERDICINÆ.

	Tetraogallus himalayensis himalayensis	*Tetraogallus himalayensis.*	*Tetraogallus himalayensis.*
	Alectoris graeca chukar.	*Caccabis chucar.*	*Caccabis chukor.*
	Francolinus francolinus asia	*Francolinus vulgaris.*	*Francolinus vulgaris.*

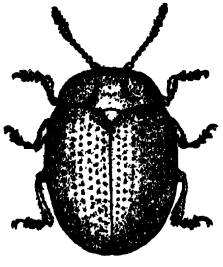
English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Eastern Wood Pigeon.	——	——	M.P. 71.
Ashy Wood Pigeon.	v. pls. 67, 68.	x. pl. 36.	viii. pls. 13, 14.
Nilgiri Wood Pigeon	——	——	viii. pls. 16, 17; xii. pl. 20.
Purple Wood Pigeon.	——	i. fig. 174.	——
Speckled Wood Pigeon.	v. pls. 64, 65, 66.	——	viii. pl. 15.
Bar-tailed Cuckoo-Dove.	v. pls. 70, 71.	i. fig. 176.	viii. pl. 19; xii. pl. 18
Northern Indian Rufous Turtle Dove.	v. pls. 72, 73, 74.	——	viii. pl. 20.
Indian Spotted Dove.	v. pls. 75, 76.	——	viii. pl. 9.
Indian Little Brown Dove.	——	i. fig. 177.	viii. pl. 8.
Indian Ring Dove.	v. pl. 77.	——	viii. pls. 9, 10.
Indian Red Turtle Dove.	v. pl. 78.	i. fig. 178.	viii. pl. 12.
Indian Bronze-winged or Green-winged Dove.	v. pl. 79.	ii. fig. 362.	viii. pls. 21, 22.
Nicobar Pigeon.	——	ii. fig. 403.	——
Common Bustard-Quail.	v. pls. 149, 150.	i. fig 188; xi. pl. 21.	viii. pl. 50.
Little Button Quail.	v. pls. 147, 151.	——	viii. pls. 48, 49.
Indian Button Quail.	v. pl. 150.	——	——
Painted Sand Grouse.	v. pl. 81.	——	viii. pl. 23.
Imperial or Black-bellied Sand Grouse.	v. pl. 80.	——	——
Common Indian Sand Grouse.	v. pl. 82.	——	viii. pls. 24, 25, 26.
Himalayan Snow Cock.	v. pls. 119. 120.	——	——
Chukar.	v. pl. 131.	——	M.P. 76. viii. pl. 33.
Indian Black Partridge.	v. pls. 124, 125, 126, 127, 128, 129, 130.	——	viii. pls. 31, 32.

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
	Francolinus francolinus melanonotus.	*Francolinus vulgaris.*	*Francolinus vulgaris.*
	Francolinus pintadeanus phayrei.	*Francolinus chinensis.*	——
	Francolinus gularis.	*Francolinus gularis.*	*Ortygornis gularis.*
	Francolinus pondicerianus pondicerianus.	*Francolinus pondicerianus.*	*Ortygornis ponticeriana.*
	Francolinus pondicerianus interpositus.	*Francolinus pondicerianus.*	*Orytygornis ponticeriana.*
	Perdix hodgsoniæ hodgsoniæ.	*Perdix hodgsoniæ.*	——
	Perdicula asiatica asiatica.	*Perdicula asiatica.*	*Perdicula cambayensis.*
	Perdicula asiatica argoondah.	*Perdicula argunda.*	*Perdicula asiatica.*
	Arborophila torqueola torqueola.	*Arboricola torqueola.*	*Arboricola torqueola.*
	Arborophila rufogularis rufogularis.	*Arboricola rufigularis.*	*Arboricola rufogularis.*
	Arborophila brunneopectus brunneopectus.	*Arboricola brunneipectus.*	——
	Tropicoperdix chloropus.	*Tropicoperdix chloropus.*	——
	Cryptoplectron erythrorhynchum erythrorhynchum.	*Microperdix erythrorhynchus.*	*Perdicula erythrorhyncha.*
Rollulus rouloul correct spelling.	*Rollulus roulroul.*	*Rollulus roulroul.*	——
	Coturnix coturnix coturnix.	*Coturnix communis.*	*Coturnix communis.*
	Coturnix coturnix japonica.	*Coturnix communis.*	*Coturnix communis.*
	Coturnix coromandelica.	*Coturnix coromandelica.*	*Coturnix coromandelica.*
	Excalfactoria chinensis chinensis.	*Excalfactoria chinensis.*	*Excalfactoria chinensis.*
	Galloperdix lunulata.	*Galloperdix lunulata.*	*Galloperdix lunulosus.*
	Galloperdix spadicea spadicea.	*Galloperdix spadicea.*	*Galloperdix spadiceus.*
	Subamily Phasianinæ.		
	Ithaginis cruentus.	*Ithagenes cruentus.*	*Ithaginis cruentus.*
	Lophophorus impejanus.	*Lophophorus impeyanus.*	*Lophophorus impeyanus.*
	Tragopan satyra.	*Tragopan satyra.*	*Ceriornis satyra.*
	Tragopan melanocephalus	*Tragopan melanocephalus.*	*Ceriornis melanocephala.*
	Tragopan blythi blythi.	*Tragopan blythi.*	——
	Lophura rufa	*Lophura rufa.*	——

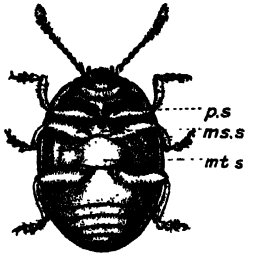
English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Assam Black Partridge.	——	i. fig. 183.	——
Phayre's Burmese Francolin.	——	i. fig. 24.	——
Kyah or Swamp Partridge.	v. pl. 132.	ii. fig. 435.	viii. pl. 38; x. pl. 42.
Southern Grey Partridge.	——	——	viii. pl. 34.
Northern Grey Partridge.	v. pl. 132.	i. fig. 184.	viii. pl. 35.
Tibetan Partridge.	v. pl. 135.	——	——
Jungle Bush Quail.	v. pl. 142.	i. fig. 186.	viii. pls. 42, 43.
Rock Bush Quail.	——	——	viii. pl. 44.
Common Hill Partridge.	v. pls. 136, 137, 138, 139, 141.	x. pl. 37.	viii. pls. 39, 41; x. pl. 43.
Blyth's or Rufous-throated Hill Partridge.	v. pls. 140, 141.	i. fig. 185.	viii. pls. 36, 37, 40.
Brown-breasted Hill Partridge.	——	ii. fig. 363.	——
Green-legged Hill Partridge.	——	ii. fig. 396.	——
Painted Bush Quail.	——	——	viii. pl. 45.
Red-crested or Green Wood Quail.	——	ii. figs. 373, 377 *a*.	——
Common or Grey Quail	v pls. 143, 144, 147.	——	——
Japanese Grey Quail.	——	i. fig. 187.	viii. pls. 46 47.
Black-breasted or Rain Quail.	v. pl. 145.	——	viii. pl. 51.
Blue breasted Quail	v. pls. 146, 148.	xi. pl 20.	viii. pl. 49.
Painted Spur Fowl.	v. pl. 118.	i. fig. 180.	——
Red Spur Fowl.	——	——	viii. pls. 28, 29, 30; x. pl. 31.
Blood Pheasant.	v. pls. 93, 94, 95, 96, 97, 98, 99.	——	——
Monal or Impeyan Pheasant.	v. pls. 84, 85, 86, 87.	——	M.P. 73.
Crimson Horned Pheasant.	v. pls. 88, 89, 90, 91 92.	i. fig. 179.	M.P. 74; v. pls 32, 33.
Western Horned Pheasant.	——	——	M.P. 74.
Blyth's Horned Pheasant.	——	——	M.P. 75.
Vieillot's Fire-backed Pheasant	——	i. fig. 181; ii. fig. 368 *a*.	——

Alternative Name.	F. B. I. 2nd Ed.	F. B. I. 1st Ed.	Jerdon.
Diardigallus diardi.	*Lophura diardi.*	——	——
Crossoptilon crossoptilon crossoptilon.	*Crossoptilon tibetanus.*	——	——
	Gennæus hamiltonii.	*Gennæus albicristatus.*	*Gallophasis albocristatus.*
	Gennæus leucomelanus.	*Gennæus leucomelanus.*	——
	(*Gennæus horsfieldii cuvieri.*)	*Gennæus horsfieldi.*	——
	Gennæus lineatus lineatus.	*Gennæus lineatus.*	——
	Gennæus melanotus.	*Gennæus melanonotus.*	*Gallophasis melanotus.*
	Pucrasia macrolopha macrolopha.	*Pucrasia macrolopha.*	*Pucrasia macrolopha*
	Pucrasia macrolopha nipalensis.	*Pucrasia macrolopha.*	*Pucrasia macrolopha.*
	Catreus wallichii.	*Catreus wallichi.*	*Phasianus wallichii.*
Gallus gallus murghi.	*Gallus bankiva murghi.*	*Gallus ferrugineus.*	*Gallus ferrugineus*
Gallus gallus robinsoni.	*Gallus bankiva robinsoni.*	*Gallus ferrugineus.*	*Gallus ferrugineus.*
	Gallus sonneratii.	*Gallus sonnerati.*	*Gallus sonneratii.*
	Polyplectron bicalcaratum bicalcaratum.	*Polyplectron chinquis.*	——
	Polyplectron malaccensis.	——	——
	Pavo muticus.	*Pavo muticus.*	——

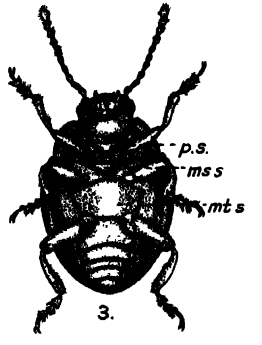
English Name.	Hodgson.	Tickell.	C. F. Sharpe.
Siamese Fire-backed Pheasant.	—	ii. fig. 406.	—
Hodgson's Eared Pheasant.	v. pl. 83.	—	—
White-crested Kalij Pheasant	v. pl. 110.	—	x. pl. 36.
Nepal Kalij Pheasant.	v. pls. 109, 111.	—	—
Cuvier's Kalij Pheasant.	—	i. fig. 67.	—
Burmese Silver Pheasant.	—	i. fig. 294.	—
Black-backed Kalij Pheasant.	v. pls. 112, 113. 114.	i. fig. 182.	x. pls. 37, 38
Koklas or Pokras Pheasant.	—	—	x. pl 34
Nepal Koklas.	v. pls. 101, 102.	—	—
Cheer Pheasant.	v. pls. 103, 104, 105, 106, 107.	—	x. pl. 35.
Common Red Jungle Fowl.	v. pls. 115, 116, 117.	—	x. pls 39, 41.
Burmese Jungle Fowl.	—	ii. fig. 368.	—
Grey Jungle Fowl.	—	—	M.P. 77 x. ; pl. 40.
Burmese Peacock Pheasant.	—	i. fig. 276.	—
Malay Peacock Pheasant.	—	ii. fig. 423 *a*	—
Burmese Peafowl.	—	i. fig. 293.	—



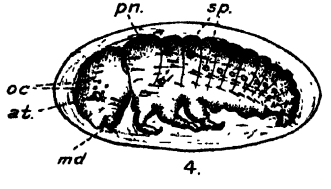
1



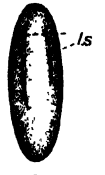
2



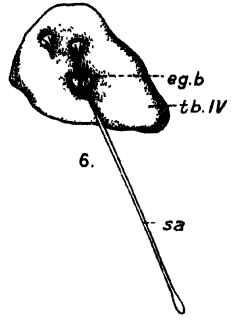
3.



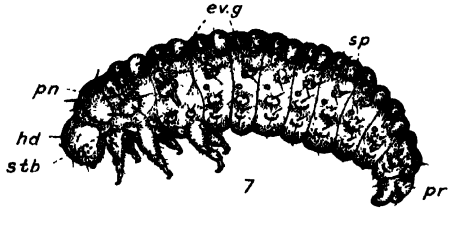
4.



5.



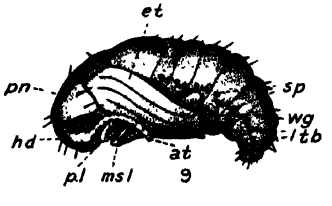
6.



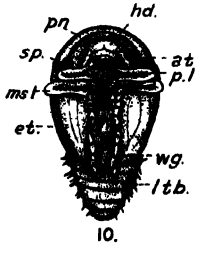
7



8.



9

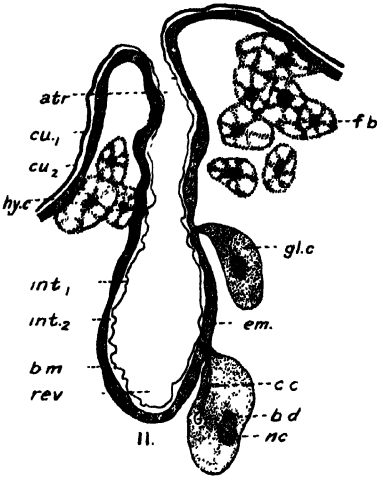


10.

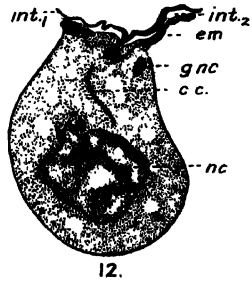
N F P del

Sons & Danielsson, Ltd London.

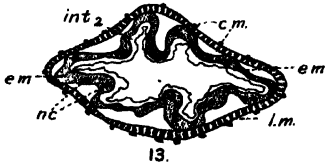
MORPHOLOGY OF THE EARLY STAGES OF PARAPHAEDON TUMIDULUS.



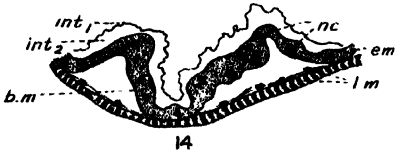
11.



12.



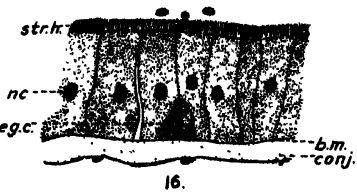
13.



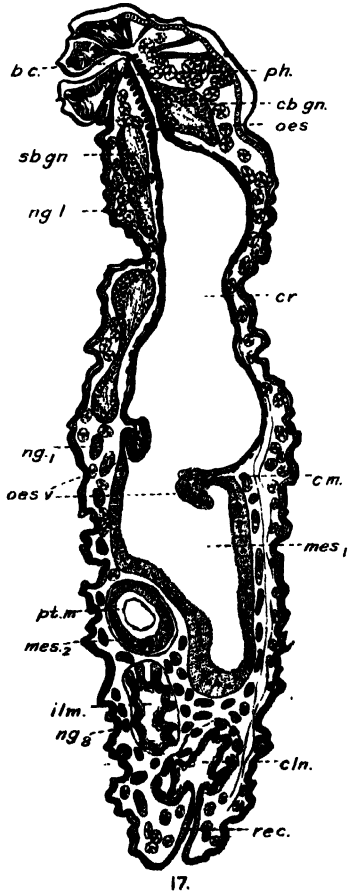
14.



15.



16.

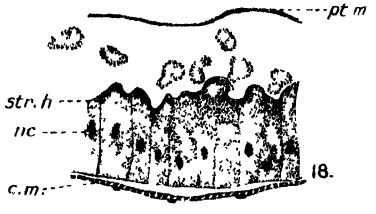


17.

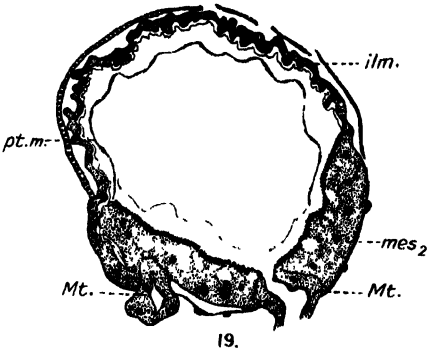
N F F del

John Bale Sons & Danielsson, Ltd London.

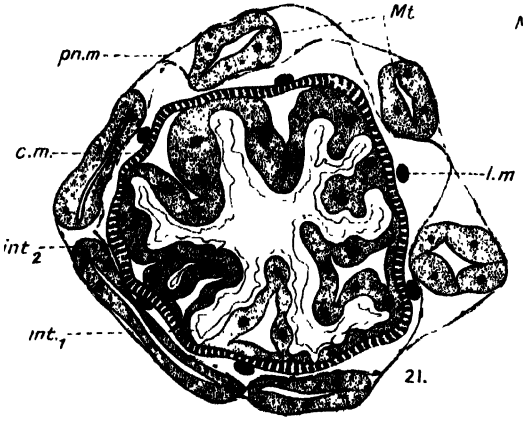
MORPHOLOGY OF THE EARLY STAGES OF PARAPHAEDON TUMIDULUS.



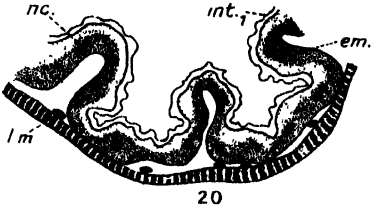
18.



19.



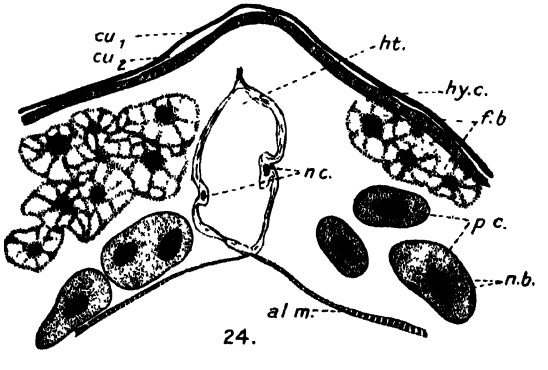
21.



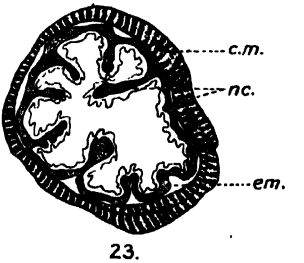
20



22.



24.

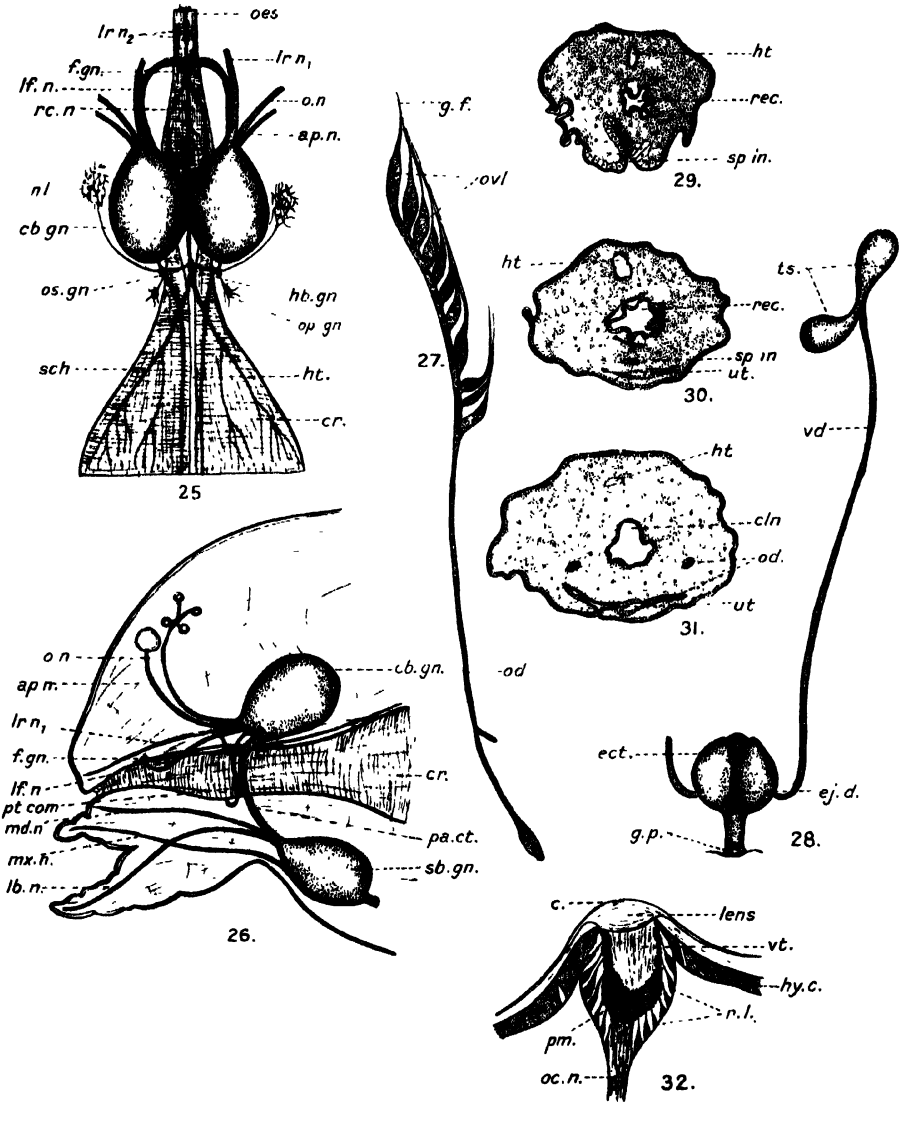


23.

N F P del

John Bale Sons & Danielsson, Ltd London

MORPHOLOGY OF THE EARLY STAGES OF PARAPHAEDON TUMIDULUS.



N F P del

John Bale, Sons & Danielsson, Ltd. London

MORPHOLOGY OF THE EARLY STAGES OF PARAPHAEDON TUMIDULUS.

STUDIES ON THE CHRYSOMELIDÆ.—PART I.

30. The Bionomics and Morphology of the Early Stages of *Paraphædon tumidulus* Germ. (Coleoptera, Phytophaga, Chrysomelidæ).

By NELLIE F. PATERSON, M.Sc., Ph.D.*

(From the Zoological Laboratories, Cambridge.)

[Received December 23, 1929 ; Read April 1, 1930.]

(Plates I.–IV.†; Text-figures 1–17.)

CONTENTS.

	Page
Introduction	627
Part I.– The Bionomics and Anatomy of the Early Stages of *Paraphædon tumidulus* Germ.	629
Material and Methods	629
Geographical Distribution	629
Food-plants and Nature of Damage	631
Life-history	631
Process of Hatching from the Egg	632
Duration of Larval Life	633
Parasites of the Larva	634
Morphology of Larvæ and Pupæ	634
A. The Pupa	634
B. The Third-stage Larva	635
External Anatomy	635
Head	635
Head-appendages	638
Endosketal or Tentorium	640
Body	640
Legs	641
Chætotaxy and Arrangement of Tubercles	641
Internal Anatomy	643
Integument	643
Eversible Glands	644
Digestive System	646
Malpighian Tubes	650
Nephrocytes	652
Circulatory System	652
Maxillary Glands	652
Muscular System	653
Respiratory System	661
Nervous System	664
Sense Organs	665
Reproductive System	666
Summary of Part I.	670
Key to Lettering of Plates	671
Bibliography	673
Explanation of Plates I. to IV.	676

INTRODUCTION.

The study of the life-history of *Paraphædon tumidulus* Germ. was undertaken at the suggestion of Dr. H. Scott, formerly Curator in Entomology in the University Museum of Zoology, Cambridge. Dr. Scott had previously made observations

* Communicated by Prof. J. STANLEY GARDINER, M.A., F.R.S., F.Z.S.

† For explanation of the Plates, see p. 676.

on the early stages of this species, but had been unable to find ova, and was desirous that the biology should be further investigated. He very kindly placed at my disposal his unpublished notes on the occurrence of the insect in various localities and his observations on its transformations, which information has proved very helpful in corroborating my own observations on its life-history.

I wish to take this opportunity of expressing my sincere appreciation and gratitude to Dr. Scott, not only for suggesting the line of investigation, but also for his assistance and kindness at the inception of the work and for the manner in which he has supervised it. My thanks are also due to Prof. J. Stanley Gardiner, M.A., F.R.S., for the keen interest he has taken in the progress of this investigation, which was carried out in the Zoological Laboratory, Cambridge, during tenure of a Union Post-Graduate Scholarship, awarded by the University of the Witwatersrand, Johannesburg. I am also indebted to Mr. Gilbert Carter and Mr. Gray, of the Botany School, Cambridge, for the identification of various botanical specimens.

The family Chrysomelidæ includes a very large number of attractively coloured insects, which are exclusively phytophagous both in their larval and adult stages. The family, as a whole, is difficult to define on account of the variety of form and diversity of structure exhibited by its members. The differences are particularly marked in the early stages, many of which, by reason of their extraordinary external appearance, seem to have little affinity for each other beyond their phytophagous habit.

In a classification of the family, based principally on adult characters, five primary divisions are usually recognized, the largest and one of the most important of which, from an economic point of view, is the *Cyclica*. Several species of this group are destructive to crops and cultivated plants. Of these may be cited the cosmopolitan genus *Phædon*, the larvæ and imagines of which have attracted considerable attention in various countries, on account of their depredations on mustard and other cruciferous plants.

The genus *Paraphædon* was erected by Dr. Sharp in 1910 for a species of *Phædon* which, in the adult stage, possesses certain definite features, entirely justifying its separation from other species. These characters may be briefly stated. In *Paraphædon* (Pl. I. fig. 2) the prosternum (*p.s.*) is carinate, the mesosternum (*ms.s.*) is excavated for the reception of the femur of the prothoracic limb, and the line of the metasternum (*mt.s.*) is anteriorly curved. In *Phædon* (Pl. I. fig. 3), on the other hand, the prosternum is not keeled, the mesosternum has no cavity for the anterior femur, and the metasternal line is directed posteriorly. It is of interest to note in this connection that, while the larvæ of *Phædon cochleariæ* F. and *Paraphædon tumidulus* present marked dissimilarities, those of *Phædon armoraciæ* L., the adult of which has slight indications of a keeled prosternum, bear a close resemblance to the larvæ of *P. tumidulus*.

The genus *Paraphædon* is now universally recognized, and comprises the single species *P. tumidulus* Germ., which has no synonyms. This species has received little attention as yet, probably on account of the fact that it is, fortunately, of no great economic importance, its attacks being chiefly confined to wild food-plants. A review of the literature, therefore, reveals very few records of its capture, and, so far as the writer is aware, there is only one reference to its life-history. In 1882 T. H. Hart bred some larvæ, but "failed to detect the vestige of an egg." No mention is made of the number of instars, and a very brief description of the larva and pupa is given. A complete account of the biology and morphology of the immature stages is, therefore, not on record.

One of the principal objects of the present paper, in addition to a study of the biology of *Paraphædon tumidulus* and the anatomy of its larva, was the investigation of certain features in the larvæ and pupæ of other typical British Chrysomelidæ, as a source of information regarding the structural and biological

relationships within the family. The study of the immature stages of insects, from the point of view of phylogeny, is of comparatively recent development, and has been largely neglected in the Chrysomelidæ. The present paper, to a certain extent, demonstrates the value of such an investigation in the Chrysomelidæ, but in view of its limitations, it is only submitted as a basis for a further and more comprehensive study of this large and interesting family.

Part I.—The Bionomics and Anatomy of the Early Stages of Paraphædon tumidulus Germ.

Material and Methods.

The chief sources of supplies of adults and larvæ for the present investigation were two isolated localities in the vicinity of Cambridge, namely, at Barton Road, Cambridge, and at Harlton, Cambs. In both of these localities the insects were very numerous in spring and summer, and consequently, in addition to extensive breeding in the laboratory, field observations on the habits and natural history of the insect were possible.

In the laboratory the insects were subjected to as natural environmental conditions as possible. They were placed on healthy plants, growing in pots, and under cover of glass cylinders with gauze tops, allowing of the entrance of air, and at the same time, preventing the accumulation of excessive moisture on the sides of the cylinders. The plants were at first placed in a room which had an almost normal outdoor temperature, but were later transferred to a cold-frame in the grounds of the laboratory. Temperature records were kept during the period of observation, in order that reference could be made to them in the event of any marked discrepancy or abnormality in development. It was found, however, that the insects responded favourably to their new surroundings, and development from egg to adult proceeded in a normal manner.

The larval morphology was investigated principally in third-stage larvæ by means of dissections and sections. The alimentary tract and the respiratory and excretory systems were traced in freshly killed specimens immersed in normal saline solution. The muscular and nervous systems were more easily followed in larvæ which had been preserved for some time in 70 per cent. alcohol. Specimens for sectioning were fixed in Bouin's solution, and the sections stained with hæmatoxylin and eosin.

Geographical Distribution.

Although usually recorded as a common and widely spread species, on account of the numbers in which it may be collected in a given locality, it was observed that *Paraphædon tumidulus* was really somewhat local and sporadic in its distribution, being limited to isolated colonies in definite and restricted areas. Deville (1921), in discussing the present-day distribution of this species as compared with its earlier distribution, remarks that, "dans les Iles Britanniques et en Barbarie (ils) présentent aujourd'hui une zone de dispersion assez continue, alors que dans l'intervalle on n'observe que des stations sporadiques." It is therefore of interest to find that indications of this irregular distribution still exist, and an examination of the various environmental factors which govern and control distribution and dispersal elucidates, in some measure, the problem of discontinuous distribution in this species.

The chief factors which control the distribution of animals in general are food-supply and climate, and in the case of phytophagous insects the former is usually decisive. This factor, however, is hardly applicable to *Paraphædon*, as its food-plants occur in a variety of topographical situations and occupy a much wider

range of habitats than the insects. Shortage or lack of food-supply cannot therefore account for its absence from some localities.

Conditions which favour the growth of the food-plants are concomitant with those controlling the development of the insects, and it is among these that an explanation of the spasmodic occurrence of the species is to be sought for. Examination of the properties of the soils tends to show that special chemical and physical constitutions are not essential to its development, as pupation and æstivation occur normally in different kinds of soils. Thus, for instance, the insects have been collected on plants growing on chalk, clay, and sandy soils, while in the laboratory they will pupate on the soil-surface or even in the bottom of empty glass vessels.

From experience in rearing the beetles in the laboratory, it is found that during pupation and æstivation excessive desiccation or moisture has to be avoided. It is, therefore, assumed that the moisture-content of the soil is one of the principal factors controlling the distribution of this species. That the distribution within a restricted habitat is primarily dependent on moisture, which to some extent is regulated by the composition of the soil, is further demonstrated by the fact that the beetles do not occur on marshy ground, but are abundant on low banks and shallow roadside ditches. They are also plentiful on high well-drained ground bordering ponds, on hill-tops and slopes, and on open heath-land, which implies that soil conditions in these localities, rather than any special topographical feature, appear to regulate its dispersal.

Other factors, such as temperature, sunshine, and rainfall, do not appear to have had any marked effect on their movements, although the adults are naturally more active in sunshine, and development proceeds more rapidly at a higher temperature.

Tower (1906) cites as one of the factors which controlled the movements of *Leptinotarsa decemlineata* in America, the habit of the adults of emerging from hibernation before their food-plant had appeared, and thus necessitating a search for food further afield. By the time the adults of *Paraphædon* appear, however, the food-plants, especially *Anthriscus sylvestris*, are well established, and there is no incentive for them to wander. This, combined with the fact that the beetles have not been observed in flight, is considered as one of the reasons for the maintenance of the colonies from year to year in the same restricted areas.

Wind is one of the chief agents, other than mechanical means of transport, assisting in the dissemination of insects which are poor flyers or are devoid of the power of flight. It is possible that it has been instrumental in the dispersion of *Paraphædon*, as no other agent which could account for its present distribution has been observed.

Deville (1921) records this species as common in Ireland and Scotland, but as very scattered in England. Its distribution in Europe is markedly irregular, as is shown by its occurrence in a few widely separated areas in France and Spain. It is also present in the mountainous and forest regions of Algiers.

In England the writer has collected it in the Hastings district, at Reigate (Surrey), and at Watlington (Oxon), in each of which localities it is abundant on *Heracleum sphondylium*. It is far from being uncommon in the Cambridge district, for, in addition to occurring in numbers on *Anthriscus* at Harlton and at Barton Road, at the latter of which places Mr. A. W. Rymer Roberts, of Cambridge, observed numerous larvæ in 1922, and kindly told the writer of their occurrence, it is common at Wicken Fen, Burwell Lode, Grantchester Meadows, on parts of the Gogmagog Hills, and at Royston. In Dr. Scott's notes there are also records of its capture on *Heracleum* at Hartlebury (Worcs), at Wye (Kent), and at Colinsburgh (Fifeshire), and of its occurrence in the Exmouth (Devon) district and in Dumfriesshire.

Food-plants and Nature of Damage.

Adults and larvæ of *Paraphædon* do a considerable amount of damage to the leaves of the umbelliferous plants, *Anthriscus sylvestris* Hoffm., *Heracleum sphondylium* L., and *H. sativum*. The larvæ feed gregariously on the leaves, and are usually sufficiently numerous to make their presence immediately noticeable. The first-stage larvæ eat small round holes in the leaves, while the later instars and the imagines devour the leaves from the margins to the midrib, often reducing the leaf to a mere skeleton. The third-stage larvæ are the most harmful, as they eat ravenously previous to entering into the quiescent prepupal phase. The adults do not markedly affect the plants, although they eat freely in early spring and after emergence from the pupal state in late summer.

There are a few interesting records of damage done by the adults to various cultivated plants, indicating that, as in the closely-allied species, *Phædon cochleariæ*, there is a possibility of their forsaking their natural wild hosts and becoming serious pests of plants which are of commercial value. In leaflet 263 of the Board of Agriculture and Fisheries, 1915, mention is made of the fact that *P. tumidulus* was injurious to celery in Yorkshire in July, 1905, and was destructive to parsley at Settle in August of the same year. In 1914 it is reported as having devoured celery leaves in Dublin, Ireland, while Maulik (1926) includes it in a list of Chrysomelidæ of economic importance on account of its attacks on potatoes in England. It is therefore evident that, as in many other phytophagous insects, this species shows a tendency to extend its range of food-plants from its original wild hosts to cultivated plants belonging, not only to the same, but also to other natural orders.

Food-test experiments in the laboratory gave negative results. Adults and larvæ transferred from *Anthriscus sylvestris* to leaves of pear, apple, mustard, and potato refused to feed on these plants, and died after a short time.

These experiments are not, however, to be regarded as proving the inability of *P. tumidulus* to change its food-plant in nature.

Life-history.

Adults (Pl. I. figs. 1 & 2) begin to emerge from hibernation towards the end of April. They are very short and convex, and are of a deep blue or bronze colour, with darker antennæ and legs. The head is coarsely punctate, while the thorax is smooth and somewhat narrower in front than behind. The elytra are finely punctured, with heavier punctures arranged in regular longitudinal striæ. They measure from 2·5 to 3·0 mm. in length. As in nearly all Chrysomelidæ, these beetles have no visible means of defence, and simulate death at the approach of danger.

Copulation takes place several times during the breeding-season, which lasts throughout the summer months. Eggs are laid two or three days after copulation, the first batches being deposited about the beginning of May. Several batches of five or six eggs are laid, and individual females in the laboratory were observed to lay from twenty-five to thirty eggs.

The eggs are placed in withered leaves and other débris at the base of the food-plant, and it is only occasionally in nature that they may be observed on the leaves. This habit of so effectively concealing the eggs probably accounts for the failure on the part of previous investigators to discover this stage. In the laboratory, females only occasionally deposited eggs in the sheathing leaf-bases and curved petioles of the food-plant.

The eggs are uniformly orange-yellow, elongate-oval, and measure about 1·5 mm. long by 0·5 to 0·6 mm. broad. In most Chrysomelidæ the eggs are provided with an additional envelope, to which Lecaillon (1898) has applied the term ***epichorion***. The epichorion is usually rather brittle and finely sculptured or

divided into a number of hexagonal areas. In *Paraphædon* it is relatively smooth, being very finely punctate and less brittle than that of some of the larger species of Chrysomelids.

The egg stage lasts from fourteen to twenty-five days, the rate of development depending chiefly on the temperature. During this period one or both ends of the egg may become conspicuously transparent, but as the embryo expands these areas disappear. The ocelli and head-appendages are visible about three days before hatching, and about twenty-four hours before this process commences the eggs present a dark greyish appearance, due to the development of pigment in the setæ, spiracles, and conspicuous dorso-lateral tubercles on the mesothorax and metathorax, all of which are readily distinguished through the egg-membranes At this stage the embryo is translucent yellow, with reddish ocelli and mandibles, and appears to become detached from the inner membranes (Pl. I. fig. 4).

Process of Hatching from the Egg.

The process of hatching has been observed in comparatively few Coleoptera, but it is well known that in many insects the embryo is provided with special structures which enable it to rupture the enveloping membranes, and so effect an opening to the exterior. These embryonic structures, or *egg-bursters*, as they have been termed, vary somewhat in form in the different orders of insects. In some insects, as exemplified by the Chrysopidæ, the Trichoptera, and Psocidæ, the egg-bursters are thickenings of the embryonic cuticle, which is shed immediately after hatching. According to Emden (1925) the egg-bursters in several Coleoptera are specializations of the dorso-lateral cuticle, and are retained throughout the first instar. In *Paraphædon* the cuticle of the meso- and metathoracic segments is produced into a pair of short, stiff, backwardly-directed spines (*eg.b.*, Pl. I. fig. 6), which are located on small, separate, dorso-lateral tubercles.

The first visible evidence of hatching is a slight movement of the embryo, followed by regular peristaltic movements, probably induced by the alternate contraction and relaxation of the body-muscles, accompanied by blood-pressure. The anterior extremity of the embryo becomes perceptibly swollen, and the thoracic segments come into close contact with the enveloping egg-membranes. During these regular sliding movements a longitudinal slit, which is first revealed by the slow erection of a seta through it, is effected on each side of the egg in the region of the thoracic egg-bursters. Further pressure is brought to bear on this part of the egg-shell by the dilated anterior extremity of the embryo, and the aperture on one side gradually lengthens to allow of the emergence of the young larva. The occurrence of a pair of longitudinal slits (*l.s.*, Pl. I. fig. 5) was noted in several species of Chrysomelidæ, and has also been described by Bertrand (1924). It is thought, as Woods (1917) has suggested, that the second slit probably lessens the rigidity of the egg-shell and facilitates the emergence of the larva. Neither of the slits extends to the extremity of the egg-shell, and, as a rule, the one on the left side is the longer. In no case did the mandibles pierce the chorion or in any way visibly assist in the passage of the larva to the exterior. In some insects, as described by Chapman (1903) in *Orina tristis* and Smith (1920) in *Corydalis cornuta*, hatching is effected by the swallowing of air-bubbles, but this phenomenon was not observed in the embryo of *Paraphædon*.

The mesonotum is the first part to protrude from the egg-shell, and is followed by the metanotum and pronotum respectively. The anterior extremity of the embryo assumes an arched appearance until the head is liberated. When this is accomplished, the head-setæ are gradually freed and directed forwards, while those of the thoracic segments are likewise raised from the body-surface and directed backwards. The posterior extremity of the larva is rather attenuated, and the anal region is slightly curved under the sternum of the preceding segments, but, as the larva moves forward, the abdomen gradually straightens.

The legs soon become liberated, and shortly afterwards the larva succeeds in withdrawing itself from the egg-shell. The whole process takes from twenty to thirty minutes.

The larva is at first of a bright translucent yellow, with slightly darkened setæ, spiracles, and thoracic tubercles, but the cuticle gradually becomes pigmented, the colour deepening until the body assumes a general blackish appearance. The head, pronotum, and the three pairs of thoracic legs are usually brilliant black, while the tubercles and setæ are of a lighter brownish-black colour.

Duration of Larval Life.

Larval life lasts for twenty to thirty days, during which period two moults are undergone.

The first instar is, as a rule, of six or seven days' duration, but may in a few instances be prolonged to eleven days. *First-stage larvæ* (Pl. I. fig. 8) measure from 1·85 to 2·5 mm. long by 0·9 to 1·00 mm. broad. The head and prothorax are large, and the legs are long in proportion to the rest of the body. These larvæ are characterized by the presence of two pairs of dorso-lateral eversible glands (*ev.g.*), situated on the meso- and metathorax. Previous to moulting into the second stage the larva attaches itself firmly to the leaf-surface by its anal extremity. Moulting or ecdysis is accomplished by the rupture of the head-capsule along the epicranial sutures, accompanied by the splitting of the body-wall along the mid-dorsal line of the thorax. After each ecdysis the larva is of a translucent yellow, similar to that of a recently hatched larva, but the colour rapidly deepens until the larva presents a general greyish-black appearance.

Larvæ of the *second instar* measure 3·00 mm. long by 1·00 mm. broad, while the head is 0·85 mm. across. The second instar may last from four to thirteen days, but the usual period is a week. In the second and third instars the short spinous egg-bursters are lacking, but their setiferous tubercles are still represented. The second and *third-stage larvæ* (Pl. I. fig. 7) possess seven pairs of eversible abdominal processes, in addition to the two pairs observed on the thoracic segments in the first instar. Third-stage larvæ are rather lighter in colour than the preceding stages, and as they mature they assume a yellowish-green body-colour, with brownish head, pronotum, and tubercles. After about nine or ten days, during which time the larvæ eat voraciously, they enter the ground to complete their transformations. They burrow about an inch or more below the surface of the soil, and there construct rounded earthen cells by contortions of the body. It is thought that the earth lining the cell is cemented together by a secretion from the maxillary glands.

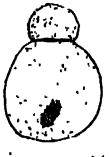
The larva spends ten days or even a fortnight within its cell, in a quiescent *prepupal stage*, before metamorphosing into a *pupa*. The body of the prepupa is somewhat arched and stout, and the insect gradually becomes less responsive to stimuli, until, owing to histolysis of the larval tissues, it is entirely unable to move. The prepupa moults in a manner similar to that observed at the end of each larval instar. The last larval skin is not retained as a covering, but is cast to one side. The pupal stage is of ten to fourteen days' duration. Normally the newly emerged beetle does not leave the pupal cell until it has assumed its full coloration, which is usually effected in a few hours.

The beetles immediately begin to feed, and may be observed in the field until the end of July or the beginning of August, when some of them go into æstivation. There is no tendency for the adults to pair after emergence from the pupal state, and consequently only one generation in the year results. They remain in concealment until the following spring, when the life-cycle is recommenced. Some adults were observed to live for two seasons, but, as a rule, they die soon after oviposition.

Parasites of the Larva.

In some districts the larvæ are heavily parasitized by *Meigenia floralis* Mg., while in other localities very few are affected. The eggs of this Tachinid are laid on the body-surface of the larval host. The larva of the parasite then bores its way into the body-cavity of the host, which succumbs in the third instar. By that time the parasite has pupated, and the larval *Paraphædon* becomes stiff and dilated, with the cuticle tightly stretched around the fly puparium, which usually effects an opening to the exterior in the antero ventral region of the dead host.

Text-figure 1.



Gregarina sp. × 233.

No other insect parasites were observed, but Dr. Scott has noted that, according to Donisthorpe, *Saprinus* adults prey on the larvæ of *Paraphædon*.

The larvæ were not examined for protozoal parasites, but on one occasion on dissecting the alimentary canal a gregarine-like organism (text-fig. 7) was observed. Gregarines are of common occurrence in Coleoptera, as has been shown by the researches of Watson (1916), but the species recorded in Chrysomelidæ are unlike that observed in *Paraphædon*.

Morphology of Larvæ and Pupæ.

A. *The Pupa.*

In life the average pupa (Pl. 1. figs. 9 & 10) measures 3·5 mm., long by 2·00 mm. across the thorax, but in preserved specimens, in which the abdomen becomes extended, the length is about 5·00 mm. The body is uniformly bright, translucent yellow at first, with short concolorous setæ. Later, the eyes, mouth-parts, antennæ, and tarsi assume a deeper pigmentation. The pupa is of the exarate type characteristic of the order, with a strongly deflexed head (*hd.*), and with the antennæ, wings, and legs free from, but closely apposed to, the body. The pronotum (*pn.*) forms a broad plate which partly covers the head. The meso-thorax and metathorax are subequal in length, and, as a rule, the shield-shaped scutellum may be distinguished mid-dorsally on the mesothorax. The abdominal segments are rather short and taper towards the posterior extremity. The elytra (*et.*) and wings (*wg.*) are curved on to the ventro-lateral surface of the body, passing between the mesothoracic and metathoracic legs. They cover the greater part of the femora of the latter pair of limbs, but they do not meet ventrally. The two anterior pairs of legs (*p.l.* and *Ms.l.*) are sharply bent at the femoro-tibial joints, which project laterally beyond the elytra. The antennæ (*at.*) are curved round the femora of the prothoracic and mesothoracic legs, and are closely applied to the surface of the elytra. The mouth-parts of the adult can be readily distinguished beneath the thin colourless pupal integument, but they, and also the antennæ and legs, present a fleshy appearance at this stage.

The ventral surface of the body is glabrous, but the dorsal surface is furnished with rather short almost colourless setæ, with regular segmental disposition. The head has three pairs of setæ arranged in two lateral rows on the vertex. The pro-thorax usually bears eight setæ on each side of the mid-dorsal line. The remaining

segments of the body have each a pair of short mid-dorsal setæ, and in most of the abdominal segments there are indications of a pair of dorso-lateral setæ. These latter setæ, however, can only be easily distinguished in the seventh, eighth, and ninth segments, in which they are relatively long and subequal to the dorsal setæ. The seventh abdominal segment is longer than the anterior segments and is rounded posteriorly. It is provided with an additional short dorso-lateral seta. The eighth and ninth segments are greatly reduced, but each bears two pairs of dorsal setæ.

In the first to the eighth abdominal segments there is a projecting lateral tubercle (*l.tb.*), which in all segments, with the exception of the first and the eighth, carries a pair of setæ. In segments 1, 8, and 9, in the latter of which the tubercle is not demarcated, there is a single lateral seta. Spiracles are present on the mesothoracic and the first six abdominal segments. The mesothoracic spiracle is large and lies anteriorly in the pleural region, immediately behind the prothoracic shield. The dorso-lateral abdominal spiracles (*sp.*) are small, concolorous with the body, and somewhat difficult to distinguish.

B. *The Third-stage Larva.*

The external and internal anatomy of the third stage larva were studied in detail.

External Anatomy.

The larva (Pl. 1. fig. 7) is of the eruciform type, with a subcylindrical body provided with three pairs of rather short, stout, thoracic legs, adapted to a terrestrial habitat. The body is divided into a head (*hd.*), three distinct thoracic, and ten abdominal segments. In the third instar the head and its appendages, the pronotum (*pn.*), the joints of the legs, and the dorsal tubercles are more strongly chitinized and darker in colour than the remaining parts of the body. The intersegmental cuticle is not deeply pigmented, but usually exhibits a division into small greyish polygonal areas. The mature larva measures 7·5 mm. long by 2·00 mm. broad, and has a yellowish-green appearance owing to the deeper coloration of the fat-body at this stage. The larvæ are highly sensitive to external mechanical stimuli, as is demonstrated by the immediate eversion of their paired dorso-lateral glands at the slightest disturbance.

Head.

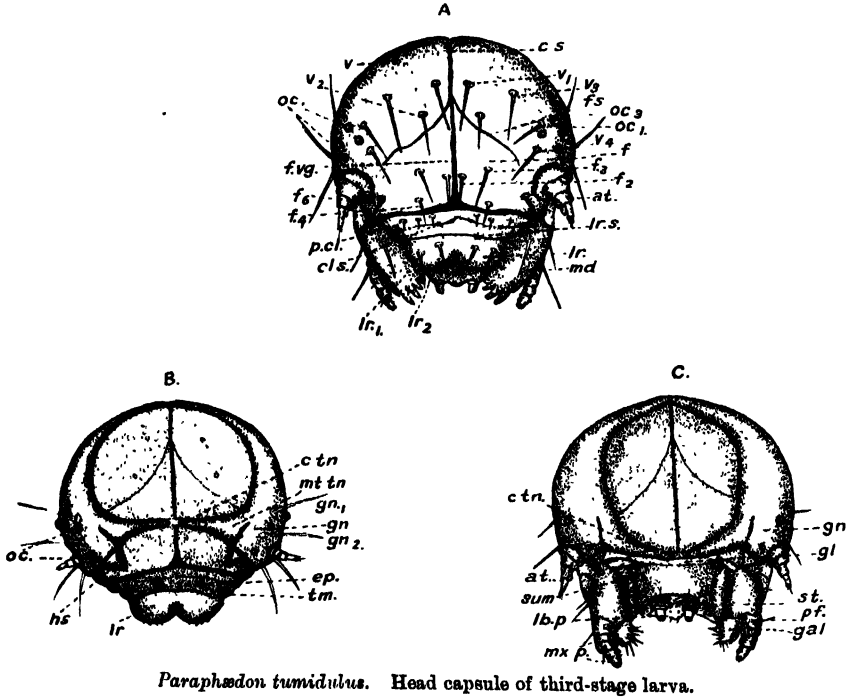
The structure of the head does not differ fundamentally from that typical of the family. It is bilaterally symmetrical and almost circular in general outline, being about as long as it is broad, and measuring 1·00 mm. across. It is held in a vertical position, and is closely approximated to the prothorax.

The *exoskeleton* of the head is composed of several sclerites, which are demarcated by distinct sutures, the whole system of sclerites forming a more or less uniformly chitinized head-capsule.

On the dorsal surface of the head-capsule (text-fig. 2, A) there is a well-defined Y-shaped *epicranial suture*, the presence of which is regarded as a primitive feature, as it is typical of generalized insects. The stem of the Y, which forms a median suture, extends from the occipital foramen to a point about one-quarter of the distance from the foramen to the anterior margin of the labrum. The *epicranial stem* or *coronal suture* (*c.s.*, text-fig. 2, A) is slightly reinforced on either side, and bifurcates proximally into two *epicranial arms* or *frontal sutures* (*f.s.*). The epicranial suture is thought, by Comstock and Kochi (1902) and other investigators, to represent the dorsal closure of the embryonic head, but Crampton (1921) considers that it is an invagination of the integument which functions as an attachment for muscles.

The frontal sutures extend almost to the base of the laterally situated antennæ (*at.*), and divide the dorsal surface of the head-capsule into a distal region, the *vertex* (*v.*), and an anterior sclerite, the *frons* (*f.*). The frons is a triangular sclerite, embraced by the frontal sutures, and extending proximally between the bases of the antennæ. It is divided longitudinally into two equal parts by a mid-dorsal invagination (*f.vg.*), which is continuous posteriorly with the epicranial stem. Anteriorly the frons is fused with the *clypeus*, from which it is, however, demarcated by a greatly strengthened *fronto-clypeal suture* (*f.cs.*). The clypeal region is rectangular, and is divided by a narrow *clypeal suture* (*cl.s.*) into a *post-clypeus* (*p.cl.*) and an *ante-clypeus*. The occurrence of a clypeal suture is another

Text-figure 2.



Paraphædon tumidulus. Head capsule of third-stage larva.

A. Dorsal aspect, × 40. B. Ventral view, with mouth-parts removed, × 50.
C. Ventral view, × 40.

indication of a primitive condition. The post-clypeus is pigmented and more strongly chitinized than the ante-clypeus, which is somewhat membranous. The dorsal articulation of the mandible occurs near the slightly projecting lateral margins of the post-clypeus.

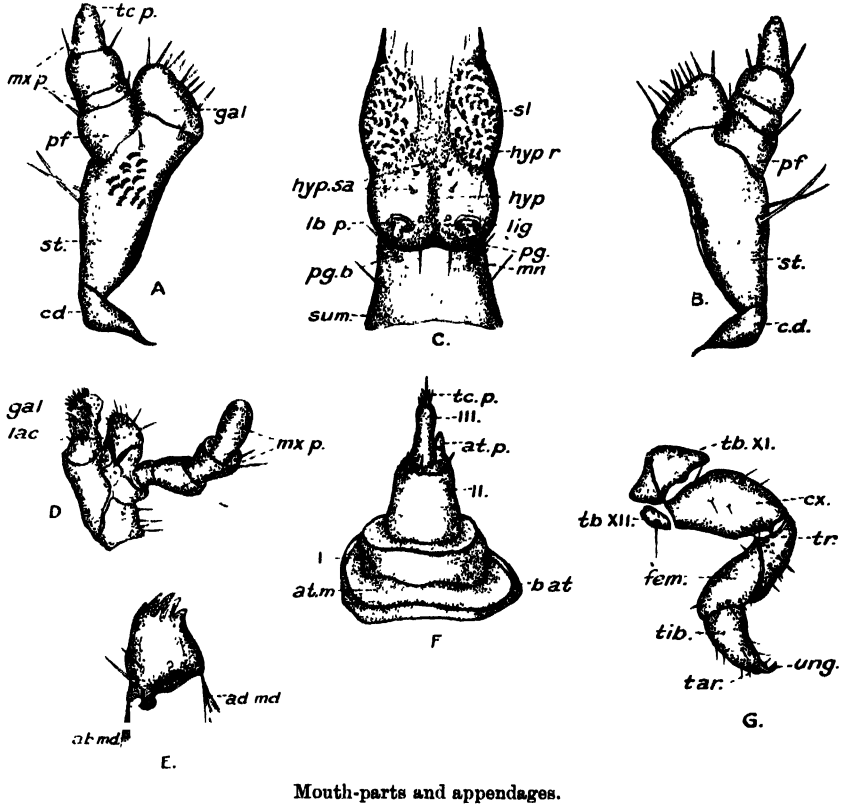
The *labrum* (*lr.*) is an unpaired sclerite which presents a bilobed anterior margin. It articulates with the ante-clypeus by means of the *clypeo-labral suture* (*lr.s.*), at each end of which there is a ventro-lateral thickening, the *torma* (*tm.*, text-fig. 2, B).

In some generalized insects the vertex is separated by an occipital suture from the occiput, which comprises the dorsal and lateral regions of the head-capsule, around the occipital foramen. In the larva of *Paraphædon* the occipital sutures

are obliterated and the occiput is not developed as a distinct sclerite. The posterior extent of the vertex is therefore indefinite. The antero-lateral regions of the head-capsule, ventral to the antennæ, are termed the *genæ* (*gn.*, text-fig. 2, B & C), which, in *Paraphædon*, are not further divided by longitudinal sutures into post-genæ. Anteriorly to the gena a small sclerite (*hs.*, text-fig. 2, B) is separated off. The ventral condyle of the mandible articulates in this region, which is therefore probably comparable with the *hypostome*.

On the ventral side of the head-capsule there is a transversely elongate region,

Text-figure 3.



Mouth-parts and appendages.

A. Dorsal aspect of left maxilla, × 106. B. Ventral aspect of left maxilla, × 106. C. Labium and hypopharynx of third-stage larva, × 106. D. Right maxilla of adult, × 106. E. Right mandible of larva, ventral aspect, × 47. F. Antenna of third-stage larva, dorsal view, × 125. G. Right mesothoracic leg of third instar, dorsal view, × 47.

the *gula* (*gl.*, text-fig. 2, C). It extends from the occipital foramen to the base of the submentum, from which it is only distinguishable by its more transparent and membranous appearance.

Ocelli.—On each side of the head there are six darkly pigmented convex ocelli (*oc.*, text-fig. 2, A & B), arranged into two groups. The dorsal group consists of four ocelli situated in the antero-lateral angle of the vertex, immediately behind the antenna. The remaining two ocelli are located ventrally on the gena. The

anterior of these is rather small and lies near the socket in which the mandible articulates.

On the dorsal surface of the head there is a number of light-coloured areas, arranged in regular groups. They mark the places of attachment on the cuticle of the cephalic muscles.

Head-appendages.

The *antennæ* (text-fig. 3, F) are situated near the antero-lateral limits of the frontal sutures. Each is a simple three-jointed structure, the base of which is surrounded by an annular thickening of the head-capsule (*b.at.*), termed the *basantenna* by Crampton (1921, A). The first joint of the antenna is relatively short and broad, and is connected with the basantenna by means of a wide, transparent, flexible membrane (*at.m.*), which allows of considerable freedom of movement, and permits of the antenna being completely retracted within the head. The second antennal segment is longer than broad, and carries three short dorsal setæ and a small peg-like proce s at the base of the third joint. The latter joint is elongate and terminates in a long median seta, which is surrounded by five shorter tactile processes (*tc p.*). In addition to the terminal joint, the broad middle segment bears an antero-ventral conical process (*at.p.*), which is probably likewise tactile in function.

Mouth-parts or Trophi.

The ventral or pharyngeal wall of the labrum is continued posteriorly as a membranous *epipharynx* (*ep.*, text-fig. 2, B), which is reinforced laterally by two delicate rod-like chitinizations, probably representing vestiges of the anterior arms of the tentorium. The epipharynx is provided with two groups of five rounded sense-organs, and on each side of its anterior border there are four or five short pointed setæ, which project from the anterior margin of the labrum.

The *mandible* (text-fig. 3, E) is a stout structure, articulating with the head-capsule by a slight dorsal and a more conspicuous ventral condyle (*con.*). The latter articulates in a socket at the anterior extremity of the gena. The mandible is further connected with the head-capsule and maxillæ by means of a delicate membrane. The mandible is of a generalized type, such as occurs in *Periplaneta* and in the larva of *Corydalis*. It has five teeth, the inner and outer of which are much reduced. The three middle teeth are longer and sharper than the other two, and their margins are slightly serrated. There are two long primary setæ on the dorso-lateral surface of the mandible. The strong adductor (*ad.md.*) and abductor (*ab.md.*) muscles are inserted on broad tendons at its inner and outer margins respectively.

The *maxillæ* (text-fig. 3, A & B) are somewhat removed from the condition found in primitive insects. In primitive Coleopterous larvæ the cardo is composed of two sclerites, the eucardo and paracardo (Crampton, 1921, *a*; and Gage, 1920). In *Paraphœdon*, however, these sclerites are fused to form a single triangular *cardo* (*cd.*), which articulates loosely with the antero-ventral region of the gena near the hypostome. The *stipes* (*st.*) is an oblong sclerite articulating proximally with the cardo and mesially with the labium. Its labial margin is strongly chitinized, and may represent the inner sclerite or parastipes of more generalized insects. Distally a shoulder-like area, the *palpifer* (*pf.*), is demarcated. The stipes and palpifer have each two long setæ, while distally on the stipes, near the base of the galea, there are two short setæ. The dorsal wall of the stipes is provided with numerous short setæ, arranged in semicircular groups, similar to those occurring on the superlinguæ.

The three-segmented *maxillary palpus* (*mx.p.*), is borne at the distal end of the palpifer. The first joint is short and broad; the second is rather longer and

bears three setæ; while the terminal segment is cylindrical, and ends in eight to ten short tactile processes (*to.p.*).

Distally the maxilla carries a single lobe or *mala* (*gal.*), which, subsequent to an investigation of the condition in other Chrysomelid larvæ, is considered to be homologous with the *galea*. It is a broad triangular structure, provided with ten sharp, stout, tooth-like setæ, which are arranged in three rows on its inner lateral border. The relative sizes of the setæ vary, but usually the proximal ones are the longest. A lacinia does not appear to be represented in the larva, although there is an analogous structure in the adult (*lac.*, text-fig. 3, D), provided with rows of setæ.

The inner lateral border of the stipes is connected with the labium by a delicate non-pigmented membrane. The *labium* (text-fig. 3, C) shows a greater departure from the primitive type than any of the other head-appendages, and bears little resemblance to that of a generalized insect. Many of its parts seem to be lacking, indicating a certain degree of specialization, which is further shown by its similarity to the labium of Coccinellid (Gage, 1920) and Noctuid larvæ (Ripley, 1923). The labium is composed of a large, proximal, rectangular sclerite, the *submentum* (*sum.*), distal to which there is a membranous, translucent, narrow area, which may be homologous with the *mentum*, although there is no distinct suture. The submentum is deeply pigmented and bears one pair of primary setæ, while there are two pairs of setæ anteriorly on the mentum (*mn.*). The *labial palpi* (*lb.p.*) are borne on a raised membranous *ligula* (*lig.*), proximal to which there is a well-chitinized semicircular sclerite (*pg.b.*), which seems to represent the fused bases of the *palpigers* (*pg.*). The latter structures are wide membranous regions on each side, between the transverse sclerite and the labial palpus. Immediately in front of each palpus, and close to the semicircular sclerite, there is a prominent seta, while there is also a short seta laterally on the sclerite.

The labial palpus is a short two-segmented appendage. The proximal segment is very short and annular, but the distal one is rather longer, cylindrical, and ends in a group of ten short colourless processes, similar to those on the terminal joint of the maxillary palpus.

The ligula, which is homologous with the fused glossæ and paraglossæ, passes imperceptibly into the hypopharynx (*hyp.*). In *Paraphædon* the hypopharynx is a large membranous lobe, distal to the labium. It extends dorsally and posteriorly to form the floor of the pharynx. A narrow chitinized sclerite (*hyp.r.*) lies longitudinally along each side of the hypopharynx, extending as far as the junction of the pharynx and œsophagus, where it meets a similar sclerite from the epipharyngeal region. The epipharynx and hypopharynx are also connected by a thin cuticular membrane. Typically the hypopharynx bears three pairs of minute setæ (*hyp.sa.*), arranged mid-dorsally behind the labial palpi.

The occurrence of a pair of dorso-lateral lobes (superlinguæ, maxillulæ, or paragnaths), associated with the hypopharynx, was first recorded in Endopterygote insects by Carpenter and MacDowell (1912) in the larvæ of *Helodes* and *Dascillus*. Evans (1921), who has investigated the condition of the hypopharynx and maxillulæ in various orders of insects, has shown that paired lobes on the hypopharynx are of general occurrence in insects, including larval forms, but that they vary greatly in structure and in their degree of fusion with the hypopharynx. Many morphologists have homologized these structures with the maxillulæ of Crustacea, but Crampton (1921 *b*) regards them as the homologues of crustacean paragnaths, and on this theory the term "maxillulæ" would be incorrect. The term superlinguæ has been used by Imms (1925), and is adopted in the present paper. In the larvæ of *Paraphædon* there is a pair of convex lateral lobes in the distal part of the hypopharynx. These lobes (*sl.*, text-fig. 3, C), which almost cover the surface of the hypopharynx, are beset with numerous

small chitinous projections, and are regarded as homologous with the superlinguæ of other insects, although they have apparently become entirely fused with the hypopharynx and have lost their appendicular appearance.

Endoskeleton or Tentorium.

In generalized insects three pairs of invaginations of the body-wall enter into the formation of the tentorium, which acts as a support for some of the head-structures and as an attachment for some of the muscles. In the larva of *Paraphædon* the tentorium is greatly reduced and presents little resemblance to that of closely related forms, such as the Coccinellidæ (Gage, 1920). The occipital foramen is divided into two by the *corpotentorium* (*c.tn.*, text-fig. 2, B and C), which is a narrow membranous bar, dorsal to the gula. It is formed by the mid-ventral extensions of the *metatentoria* (*mt.tn.*, text-fig. 2, B) or dorsal arms of the tentorium. The posterior arms are not clearly defined, but they are probably represented by annular thickenings along the dorsal and lateral margins of the occipital foramen. The anterior arms or pretentoria seem to be absent.

In correlation with this reduction in the number of tentorial invaginations several additional infoldings have taken place, giving the necessary support which would otherwise have been afforded by the tentorium. The mid-dorsal invagination in the frons, and the greatly strengthened lateral portions of the fronto-clypeal suture, represent such secondary infoldings, and the latter of these may include parts of the anterior tentorial arms, which in other forms are usually located along this suture.

Body.

The body is slightly convex dorsally and somewhat flattened ventrally. The thoracic segments are broad and long, but those of the abdomen are short and taper gradually towards the caudal extremity. The prothoracic tergum (*pm.*, Pl. I. fig. 7) is composed of a broad rectangular sclerite, formed no doubt by the fusion of dorsal tubercles, such as occur on other segments of the body. The pronotum is divided mid-dorsally into two by a slender longitudinal line, which is continuous anteriorly with the epicranial stem of the head-capsule and posteriorly with a similar line in the mesothoracic and metathoracic segments. It is along this line that the larval cuticle is ruptured during ecdysis. The pleural region is greatly reduced in the prothorax, but a single rounded tubercle (*s.tb.*), situated ventro-laterally to the pronotum, may represent a subspiracular sclerite. Between the coxæ of the legs there is a single median ventral sclerite, which may be homologous with the eusternum of primitive adult insects.

The remaining body-segments are characterized by the occurrence of a number of pigmented chitinized areas, arranged typically into two transverse rows on the tergum and a somewhat discontinuous single row on the sternum.

Dorso-laterally in the mesothorax and metathorax, and rather more dorsally in the first seven abdominal segments, there are paired eversible processes (*ev.g.*, Pl. I. fig. 7), each of which protrudes through an aperture in a conspicuous tubercle. The glands on the thoracic segments are larger than those on the abdominal segments, and are the only ones present in the first instar.

In the eighth and ninth abdominal segments there are single tergal plates formed by the fusion of dorsal tubercles. The sternites in these two segments are shorter than their corresponding tergites, and, in consequence, the anus takes up a ventral position The tenth abdominal segment or anal proleg (*pr.*, Pl. I. fig. 7) is small and membranous, and is scarcely visible from the dorsal surface. It acts as a sucker-like organ and aids in locomotion. The anus is a somewhat Y-shaped aperture, situated at the posterior extremity of the anal proleg.

There are nine pairs of uniforous spiracles (*sp.*, Pl. I. fig. 7). The mesothoracic

spiracle is situated on a tubercle lying in the anterior half of the pleural region. In a corresponding position in the metathorax there is a small dark plug of chitin, representing a rudimentary spiracle. The abdominal spiracles are arranged laterally in the anterior half of the first to the eighth segments inclusively. Each spiracle has a dark circular peritreme, which is slightly raised above the surface of the body.

Legs.

The paired thoracic legs (text-fig. 3, G) are similar in general appearance and chætotaxy, and differ only in their respective sizes. Each leg consists of five joints, which may be comparable with the leg-joints of adult insects, although several investigators are of a contrary opinion. Packard (1898), Girault (1905), and others have demonstrated that the adult legs arise from histoblasts at the bases of the larval legs, and that during development they scarcely project within the larval legs. In the pleural region at the base of each leg there is an anterior triangular plate (*tb.*XI.) and a posterior rounded tubercle (*tb.*XII.), which may respectively be comparable with the episternum and epimeron of adult insects, as is interpreted by Crampton (1918) in various larval insects, including several species of Coleoptera. Böving and Champlain (1920) are of the opinion that the similar sclerites in Clerid larvæ are not the homologues of the adult structures, and have referred to them as the pre- and post-hypopleural chitinizations. In the prothorax of the larva each of these sclerites is provided with one seta, but in the meso- and metathorax only the posterior tubercle is setiferous and bears a single seta.

The *coxa* (*cx.*) is a short, broad, subcylindrical joint, articulating with the ventral body-wall. Its inner (ventral) surface is shorter and more membranous than its outer (dorsal) surface. The second segment or *trochanter* (*tr.*) is short and triangular in outline, and bears four conspicuous setæ and several small round sensory pores. Its margins are deeply pigmented and strongly chitinized. The *femur* (*fem.*) and *tibia* (*tib.*) are subequal in size. The latter narrows towards its distal end, where it articulates with the *tarsus* (*tar.*), which consists of a single somewhat triangular segment, furnished with a sharp sickle-shaped claw (*ung.*) and one long seta.

Chætotaxy and Arrangement of Tubercles.

The term *tubercle* is applied in a general way to the chitinized, deeply pigmented, segmentally arranged areas which are furnished with one or several setæ. The disposition and number of these tubercles, in conjunction with the relative number of primary setæ, is of great systematic importance, and it has therefore been necessary to enumerate the tubercles and adopt a nomenclature which will be applicable to Chrysomelid larvæ in general. The tubercles are designated by Roman numerals, and numbered from the mid-dorsal to the mid-ventral line. Typically each tubercle should bear one seta, but owing to specialization some of the tubercles have presumably coalesced, and in some cases the number of setæ has become reduced.

The tubercles and setæ in a typical segment, as exemplified by any of the anterior abdominal segments, are arranged into a *dorsal group* (I.–IV.) extending from the mid-dorsal line to the large "gland"-tubercles (*dl.tb.*, text-fig. 4). The latter tubercles in the meso- and metathoracic segments lie in the alar region, but, as similar tubercles occur in the abdomen, the term *dorso-lateral* may be applied to them. They are thought to represent a fusion of a pair of anterior and a pair of posterior tubercles (V.–VIII.). Projecting laterally in the pleural region of the abdominal segments there is a large *subspiracular* tubercle (*s.tb.*, text-fig. 4). In the mesothorax there are two single tubercles in a similar position, and the spiracle is located antero-dorsally on the proximal tubercle. In the abdomen the spiracles

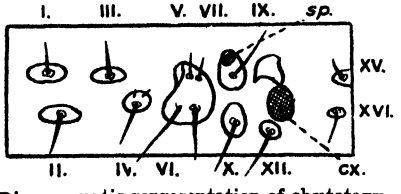
have migrated dorsally and the two subspiracular tubercles have fused. Somewhat ventral to these tubercles there is another large *pleural tubercle* (*pl.tb.*), which is represented in the thoracic segments by the pair of sclerites at the base of the coxa. The tubercles on the sternum are arranged into a *ventro-lateral* group (*vl.tb.*, XIII., XIV. XVI.) on either side of a *ventral* group (*v.tb.*, XV.), which extends transversely across the mid-ventral line and lies in front of the ventro-lateral group.

In the meso- and metathorax the disposition of the tubercles and setæ is somewhat modified owing to the presence of legs, but there is a distinct correlation between it and the arrangement in a typical abdominal segment The homologies of the setæ on the pronotum are somewhat obscure, but an attempt is made to correlate them with the setæ of other segments.

Most of the primary setæ are long, slender, and hollow, and have a somewhat trumpet-shaped free extremity. Some, however, are microscopic and taper to a sharp point.

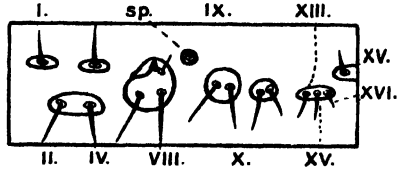
The setal arrangement is remarkably constant throughout larval life, and few, if any, secondary setæ are developed in the second and third instars. The following plans and remarks on the chætotaxy therefore suffice for all instars :—

Text-figure 3 *a*.



Diagrammatic representation of chætotaxy of mesothorax.

Text-figure 3 *b*.

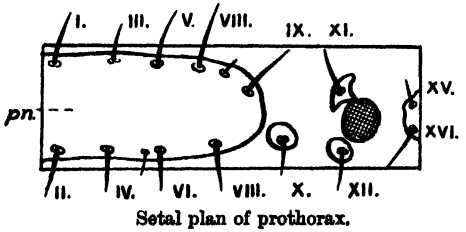


Setal plan of a typical abdominal segment.

From the foregoing plans it is evident that the arrangement of the tubercles and their corresponding setæ in the mesothorax is remarkably similar to that of a typical abdominal segment. The principal differences to be noted are the separation of tubercles II. and IV. in the mesothorax and the fusion of tubercle IX. with X. and also XI. with XII. in abdominal segments. In the thorax tubercle IV. bears two very short anterior setæ, but only one long seta is present in abdominal segments. In all segments tubercles (V.-VIII.) bear two long and two very inconspicuous setæ, representing the four setæ present on separate tubercles in a hypothetical condition.

On each side of the pronotum there are ten setæ arranged along the margins as follows:—

Text-figure 3 *c*.

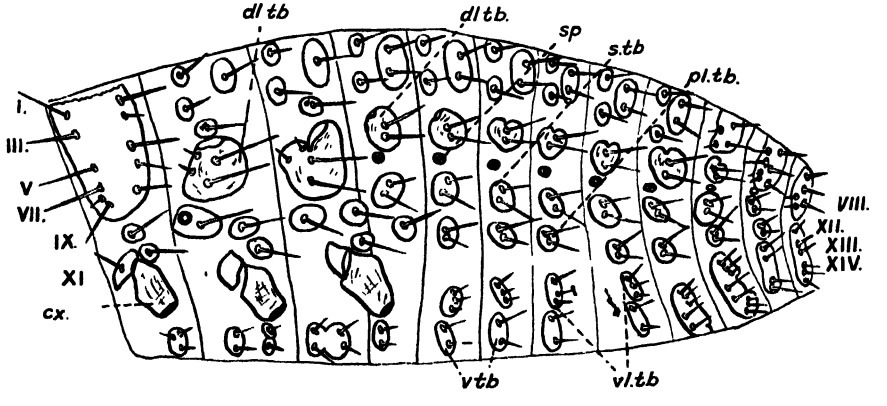


Setal plan of prothorax.

There is one additional short dorsal seta in the posterior row, but otherwise the arrangement conforms to that of other segments. Seta X. is located posterolaterally to the pronotum, and, as in all Chrysomelid larvæ, there is an insignificant seta in the antero-lateral angle of the pronotum between setæ VII. and IX.

In the posterior abdominal segments the tubercles lie closer together on account of the narrowing of the body towards the anal extremity. In consequence of this, the dorsal tubercles in the eighth and ninth segments coalesce to form single tergites, while the ventral sclerites also become reduced. In the eighth segment all the dorsal setæ usually persist, but the ventral sclerite and its pair of setæ (XV.), and also seta XVI., are absent. The tergite in the ninth abdominal segment appears to represent a fusion of the dorsal, dorso-lateral, and subspiracular tubercles, with the suppression of setæ I., IX., and X. Ventrally in segment 9 the single short sclerite bears three pairs of setæ (XII., XIII., and XIV.).

Text-figure 4.



Chætotaxy and arrangement of tubercles in the first instar, × 53.

The setæ are also definitely arranged on each of the sclerites of the head-capsule, but, as the head represents a fusion of several somites, the setæ cannot be homologized with those of the body. Following Dyar's, and, later, Ripley's (1923) system of enumeration of the head-setæ in lepidopterous larvæ, the setæ are designated by an abbreviation for the name of the sclerite on which they are located, and are numbered from the dorsal to the ventral surface by Arabic numerals. This system has also been applied to the setæ situated near the dorsal ocelli, although a separate ocellar sclerite is not demarcated. The setal arrangement on the head of *Paraphædon* (text-fig. 2) is fairly typical of the family, but certain of the setæ present in the genus *Chrysomela* are absent in *Paraphædon*.

Internal Anatomy.

Integument.

The body-wall is composed of an outer chitinous cuticle and an inner layer of small, uniformly cuboidal, hypodermal cells (*hy.c.*, Pl. II. fig. 11; Pl. III. fig. 24), resting on a delicate basement-membrane (*b.m.*). The cuticle comprises two layers of chitin (*cu.*$_1$ and *cu.*$_2$), which are distinct in most parts of the body. The outer (primary) layer is pigmented, while the inner (secondary) layer is colourless and exhibits a laminate appearance. The macrotrichia are secreted by special trichogenous cells of the hypodermal layer. They are sensory in function, being supplied by nerve-cell endings, which are somewhat difficult to distinguish in sections of the integument.

Eversible Glands.

It is well known that metameric cutaneous glands are of frequent occurrence in larval insects. Coleopterous larvæ, and notably those of the Chrysomelidæ, are furnished with hypodermal glands of various kinds which usually fall under the category of repugnatorial organs (Candèze, 1874; Wade, 1921). Such glands are highly developed in the larva of *Melasoma populi*, in which form they emit a whitish pungent secretion. Their structure has been investigated by various morphologists, notably Claus (1862) and Berlese (1909), while Garb (1915) gives an excellent account of the glands in *Melasoma lapponica*.

In the second- and third-stage larvæ of *Paraphædon* there are nine pairs of eversible glands, arranged dorso-laterally on the meso- and metathorax and the first seven abdominal segments. When the larva is disturbed these processes are everted and have the appearance of small spherical vesicles, containing a clear translucent fluid, within which one or two refractive whitish bodies may be distinguished. The processes remain everted for several seconds, and are then withdrawn, usually simultaneously, into the body-cavity. The larva is capable of everting its glands several times in succession, but great variation in the degree of response to stimuli may be exhibited. As a rule, the third-stage larvæ are the most sensitive.

No appreciable odour is emitted by the glands of *P. tumidulus*, and their efficacy as repugnatorial organs is somewhat obscure. No doubt the sudden eversion of the glands repels many predatory forms, and perhaps a delicate and highly volatile odour, perceptible only to other insects, is emitted.

Histology and Physiology of the Glands.

Each gland (text-fig. 5 & Pl. II. fig. 11) consists of a deep reservoir, which is an invagination of the dorso-lateral integument. The gland, which in a retracted condition lies embedded in the fat-body dorsal to the notopleural muscles, is divided into a short wide anterior atrium (*atr.*), from which the large sac-like reservoir (*rev.*) depends. The epithelium (*em.*) of the gland is directly continuous with the hypodermal cellular layer, and the chitinous intima lining the gland is likewise a continuation of the cuticle. The chitinous intima of the atrium is non-pigmented and transparent, but that of the reservoir exhibits numerous small, pigmented, polygonal areas. The primary or outer intima ($int._1$) is thrown into a number of small projections, while the secondary intima ($int._2$), which is rather broader, has a laminate appearance.

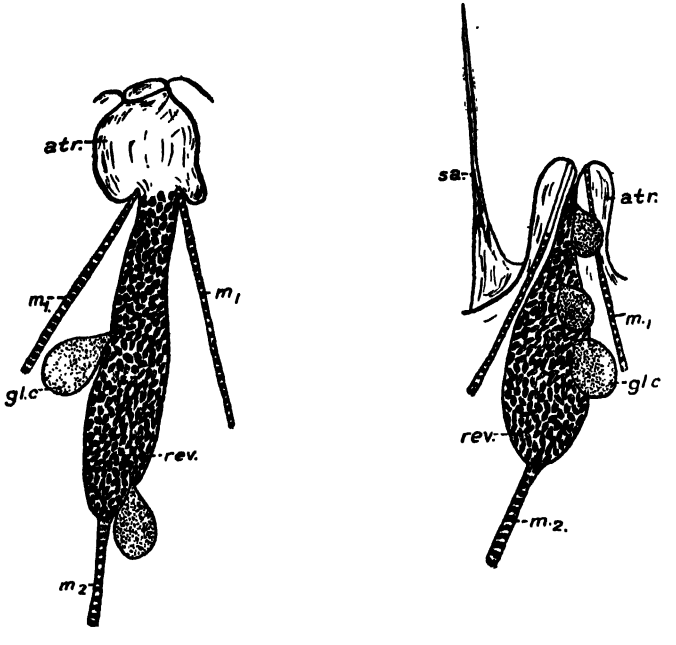
The epithelial cells are small, cuboidal, and somewhat irregular. The cytoplasm is finely granulated and the nucleus is relatively large and contains several coarse, deeply staining chromatin granules. A delicate basement-membrane (*b.m.*) supports the epithelial layer. The gland is controlled by two sets of muscle-fibres. The first comprises a pair of muscles ($m._1$) arranged one on each side of the reservoir They are inserted at the junction of the atrium and reservoir, and regulate the evagination of the proximal region of the gland. At the base of the reservoir there is a single muscle ($m._2$) which maintains the reservoir in position within the body-cavity. The muscles are attached to the ventro-lateral body-wall at the points of attachment of various other segmental muscles.

The eversion of the gland is effected by blood-pressure, resulting from the contraction of the body-muscles when the insect is disturbed. The muscles of the gland, on the other hand, relax, and the gland is forced out by means of the pressure exerted on its walls, the blood passing between the hypodermal layer of the body-wall and the epithelial layer of the atrium of the gland. The atrium alone is everted, for, when the muscles ($m._1$) which are attached to its base have reached their limit of relaxation, further protrusion of the gland beyond their insertion is rendered impossible. The blood-pressure against the everted wall of the

atrium and the anterior walls of the reservoir tends to give to the gland its characteristic globular shape, and at the same time is sufficient to close the aperture of the reservoir, preventing the excessive discharge of its fluid-contents. When the peripheral body-muscles relax the blood-pressure is reduced and the gland is withdrawn into the body-cavity by the contraction of its own muscles.

The whitish objects observed beneath the cuticle of an everted gland are large glandular cells (*gl.c.*, text-fig. 5, & Pl. II. fig. 11), which are attached to the inner wall of the reservoir. As a rule, only three glandular cells are observed along the mid-dorsal wall of each gland, the anterior of these lying near the junction of the atrium and reservoir, being the one which is visible through the cuticle of the everted atrium. Each glandular cell (Pl. II. fig. 12) is usually subspherical

Text-figure 5.



Eversible glands, × 100.

A. Retracted. B. Everted.

and has a large, central, round or oval nucleus (*nc.*) which contains coarse, deeply staining chromatin granules, arranged near the periphery. The cytoplasm is finely granular and may be vacuolated. A vacuolated condition is probably indicative of an active secretory phase, and is not always noticeable. There is a very short and narrow communicating canal (*c.c.*, Pl. II. figs. 11 & 12) between the glandular cell and the reservoir. This canal is continuous with the intima of the reservoir, and is believed to be chitinous in nature. It is usually sharply differentiated from the cytoplasm of the glandular cell, and its walls do not appear to stain with hæmatoxylin or eosin. It passes into the glandular cell, where it ends in a slight bulbous dilation (*bd.*, text-fig. 11), which is usually situated within a vacuole anterior to the nucleus. On either side of the entrance of the canal into the glandular cell there is a small, oval, deeply staining nucleus

(*g.nc.*, Pl. II. fig. 12). These latter nuclei are larger than those of the epithelial cells of the reservoir, and, although no cell-boundaries are visible, it is possible, as Garb (1915) has suggested, that they are the nuclei of guard-cells which, perhaps, secrete the chitinous lining of the canal.

The liquid secretion of the glandular cell is passed by means of the communicating canal into the reservoir, from whence it may be ejected at will by the larva. In the laboratory, however, none of the larvæ were observed to discharge any droplets from their eversible processes.

The basement-membrane (*b.m.*), supporting the epithelium of the gland, is continued over the surface of the glandular cell, which has therefore every evidence of being a much enlarged and specially modified hypodermal cell. The glandular cells vary in size from 0·09 mm. to 0·17 mm., those of the thoracic segments being larger than those occurring in abdominal segments.

Digestive System.

The alimentary tract is relatively shorter and less convoluted than that of typical herbivorous insects, but three primary divisions into fore-, mid-, and hind-intestines are easily recognizable (text-fig. 6).

Fore-intestine.

No apparent histological differentiation marks the transition between the layers comprising the integument and those of the fore-intestine. The *buccal cavity* (*b.c.*, Pl. II. fig. 17) is lined by a thickened chitinous intima which is continuous with the cuticle. The epithelial cells, which greatly resemble but are slightly longer than the hypodermal cells, rest upon a delicate structureless basement-membrane.

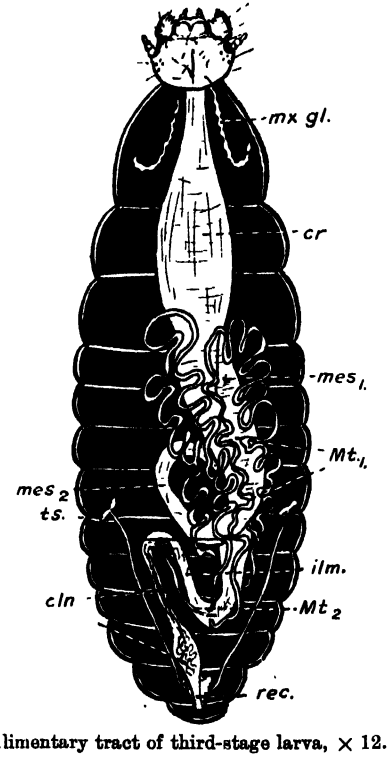
The buccal cavity leads into a short *pharynx* (*ph.*, Pl. II. fig. 17), which is bounded antero-dorsally by the epipharynx and ventrally by the hypopharynx. There is no histological difference between the posterior region of the pharynx and the *œsophagus*. The former region lies immediately proximal to the brain and is characterized by the insertion of paired dilator muscles which arise from the dorsal wall of the head-capsule. The œsophagus (*oes.*, Pl. II. fig. 17) is a narrow tube which passes below the brain and extends as far as the anterior border of the prothorax. In each of these divisions the walls (Pl. II. figs. 13 & 14) are thrown into a series of from four to six longitudinal folds, which project into the lumen of the canal. The primary intima ($int._1$) is brownish and is provided with numerous sharp tooth-like projections. The secondary intima ($int._2$) is broader and somewhat lamellar in appearance. The epithelial cells (*em.*, Pl. II. figs. 13 & 14) are large and the cell-boundaries are rather well defined. The cytoplasm seems to be finely granulated, and the nuclei (*nc.*) are large and contain coarse chromatin granules. A delicate structureless basement-membrane (*b.m.*) supports the outer surface of the epithelial cells, which are further surrounded by two layers of muscle-fibres. The inner longitudinal muscles are poorly developed, but the circular muscles (*c.m.*) comprise an almost continuous layer of strong fibres, lodged in a sheath of connective tissue.

The œsophagus passes gradually into the *crop* (*cr.*, text-fig. 6, and Pl. II. fig. 17), which is a thin-walled, distensible, piriform chamber, lying in the three thoracic segments. The transition from œsophagus to crop is accomplished by a gradual flattening of the intima and epithelium, accompanied by a marked reduction in the size of the circular muscles. The intima of the crop is thrown into minute folds, in which primary ($int._1$, Plate II. fig. 15) and secondary layers can be distinguished. The epithelial cells are usually difficult to distinguish on account of their extreme reduction, but their presence is indicated by small oval nuclei (*nc.*), which stain less deeply than those of the epithelial cells of the œsophageal region. The

longitudinal and circular muscles are much weaker than those of the œsophagus, and the fibres in each of the layers are connected by numerous anastomoses.

At its distal extremity the wall of the crop is reflected upon itself for a short distance to form a slight *œsophageal valve* (*oes.v.*, Pl. II. fig. 17), which projects into the anterior region of the mesenteron. The epithelial cells of the œsophageal valve become progressively higher, and pass almost imperceptibly into those

Text-figure 6.



Alimentary tract of third-stage larva, × 12.

characteristic of the mesenteron. The intima is continued over the inner surface of the valve, but ceases at the beginning of the mid-intestine. The valve is insufficiently developed to close the aperture between the fore- and mid-intestines, but the circular muscles (*c.m.*) in this region are greatly strengthened, and serve as contrictors, which reduce the lumen of the alimentary tract and, to some extent, prevent the regurgitation of food into the crop.

Mesenteron.

The mid-intestine or mesenteron is the longest part of the alimentary canal, and is divisible morphologically, and probably also physiologically, into two distinct regions. A wide proximal region (*mes.*$_1$, text-fig. 6 & Pl. II. fig. 17) extends from the œsophageal valve at the posterior border of the metathorax to the fifth abdominal segment, where it narrows considerably. The second or distal region of the mesenteron (*mes.*$_2$), which follows, bends sharply to the left, and pursues an almost straight course anteriorly to the middle of the third abdominal segment,

in which it redoubles upon itself and passes backwards below the proximal region as far as the seventh abdominal segment.

Histologically the mesenteron is distinguished from the fore-intestine by the absence of an intima, which seems to have been replaced by a striated hem or border on the inner surface of the epithelium. In the mesenteron the epithelial cells are large and columnar, and their boundaries are well demarcated. The muscle-layers are poorly developed and the disposition of the two layers is the reverse of that obtaining in the fore-intestine, the slender longitudinal muscles being placed outside the circular layer. The histological structure of the two divisions of the mesenteron exhibits several well-marked differences, which suggest the possibility of a differentiation into two distinct physiological regions.

In the proximal region (Pl. II. fig. 16) the striated border (*str.h.*) is well defined and sharply demarcated from the cytoplasm. The striæ have the appearance of relatively long closely-apposed filaments, arising from basal granules situated near the inner border of the cytoplasm. In the resting phase the surface of the striated border is fairly regular, but during the active secretory phase granular balls of secretion are elaborated by the epithelial cells. These balls of secretion pass through the striated border into the lumen of the mesenteron, often rupturing the striated border in the process.

The cytoplasm of the epithelial cells is finely granular, and may be slightly fibrillar at its outer border, which rests on a clearly defined basement-membrane (*b.m.*). The nuclei (*nc.*) are median in position. They are large and round and contain deeply staining chromatin granules, but they have no crystalline structures, such as were observed in *Tenebrio molitor* by Frenzel (1882). At the base of the ordinary epithelial cells there are wedge-shaped groups of small regenerating cells (*reg.c*), which have proportionately large nuclei. Between the basement-membrane and the circular muscles a layer of fibrillar connective tissue (*conj.*) is occasionally observed in the proximal chamber of the mesenteron.

The lumen of the distal division of the mesenteron (*mes.*$_2$, text-fig. 6, Pl. II. fig. 17) is reduced, and the epithelial cells are more elongate than those of the proximal division. A striated border (*str.h.*, Pl. III. fig. 18) is present, but it is shorter and not as sharply differentiated from the cytoplasm as it is in the proximal region. The cell-boundaries are less clearly defined, and the cytoplasm, especially that towards the inner border, exhibits a more vacuolated condition than is to be observed in the anterior region. The nuclei are large and oval and are located towards the bases of the cells. At the inner edge of the epithelium large, irregular, vacuolated balls of secretion are given off.

The mesenteron is the most important part of the alimentary canal from the point of view of digestion, and detailed accounts of its histology and physiology in many insects have been published. In most insects the dual functions of secretion and absorption are performed by all the cells of the mesenteron without any visible differentiation into two physiological regions. In the larva of *Ptychoptera*, however, van Gehuchten (1890) distinguishes between large, proximal, secretory cells, and equally large, distal, absorptive cells. It would appear that in *Paraphædon* a somewhat similar physiological differentiation into anterior, secretory, and posterior absorptive cells obtains, while it is also possible that, in the distal region of the mesenteron, the functions of liquid secretion and absorption are performed simultaneously.

Peritrophic Membrane.

The occurrence of a peritrophic membrane—a term proposed by Balbiani (1890) for an internal envelope surrounding the ingested food in the lumen of the mesenteron—has been the subject of much speculation and controversy in regard to its origin and function. Chatton (1920) describes its formation and structure in *Drosophila* and *Daphnia*, and he and Vignon (1901) have summarized the

various interpretations regarding its formation in different Arthropoda. The general opinion is that it is elaborated by special cells in the region of the œsophageal valve, but its mode of formation may vary greatly in different species. The presence of this problematic membrane has been recorded in relatively few coleopterous larvæ, but it is of general occurrence in larval Diptera (Imms, 1907; Keilin, 1917; Puri, 1925) and in many other larval and adult insects (Martynow, 1904), in most of which it seems to arise as a product of secretion of cells at the junction of the fore- and mid-intestines. Voinov (1898) is of the opinion that in the larvæ of Odonata it is not a special product of the valvular region, but that it represents the striated plate sloughed off after the elaboration of the balls of secretion.

In the larva of *Paraphædon* a continuous peritrophic membrane is not recognizable in the proximal division of the mesenteron, but in the distal division there is a definite colourless membrane (*pt.m*, Pl. II. fig. 17, & Pl. III. fig. 18), which also extends into the first part of the hind-intestine. Such a membrane can hardly have been produced by the cells in the region of the œsophageal valve, as the large proximal chamber of the mesenteron intervenes between the valve and the beginning of the peritrophic membrane. Its origin is not clear, but its function seems to be closely associated with the physiological nature of the epithelial cells in the two regions in which it is developed. In both of these parts of the intestine the cells are principally absorptive in function, while in the distal region of the mesenteron they may at the same time be secretory. In the anterior region of the mesenteron the products of secretion come into direct contact with the ingested food, while in the distal division the peritrophic membrane intervenes between the food-contents and the liberated balls of secretion. Gehuchten (1890), Vignon (1901), and van Gorka (1914) have suggested that the digestive fluids are able to diffuse through the peritrophic membrane. Imms (1907) is also of a similar opinion in regard to the peritrophic membrane in the larva of *Anopheles*, and Chatton (1920) concludes that it probably acts as a dialyser. The theory of osmosis presents no great difficulties, as it is well known that even the chitinous intima in the hind-intestine is permeable to some solutions (van Gorka, 1914). It is therefore possible that in *Paraphædon* the peritrophic membrane acts as an osmotic membrane, and allows of the constant interchange of liquids between the epithelial cells and the food contents of the intestine.

Hind-intestine.

The junction of the mesenteron and the hind-intestine is marked by a very slight constriction immediately distal to the exit of the Malpighian tubes. The hind-intestine is divisible into three principal parts—the ileum, colon, and rectum. Poyarkoff (1910) in *Galerucella* and Woods (1918) in *Altica* recognize four divisions, the ileum in these forms being histologically divisible into two separate parts. In *Paraphædon*, however, the histological differentiation of the two parts is not sufficiently important to merit their separation as distinct regions of the hind-intestine.

The *ileum* (*ilm.*, Pl. II. fig. 17, text-fig. 6) begins in the seventh abdominal segment and passes anteriorly to the fourth or fifth segment, where the intestine turns sharply to the left and, reversing its course, it continues posteriorly as the colon (*cln.*). The colon is at first a relatively narrow tube, but in the seventh and eighth abdominal segments its walls become thin, and the tube presents an inflated appearance. Posteriorly, at the beginning of the ninth abdominal segment, the colon joins the rectum (*rec.*), which is a straight narrow tube opening at the extremity of the anal proleg.

In the anterior part of the ileum the epithelium is flattened and the intima, which reappears at the commencement of the hind-intestine, is thrown into numerous small projections. As the ileum (Pl. III. fig. 20) continues, the cells

become larger and the lumen of the intestine is reduced by the projection into it of about six longitudinal folds of the epithelium and its chitinous intima. The cells are irregularly cuboidal and their boundaries are ill defined. The cytoplasm is differentiated into a deeply staining basal layer surrounding the large round nuclei, and an outer layer which stains less deeply and is more or less fibrillar and vacuolated. This condition of the cytoplasm may be correlated with its absorptive function. The circular muscles are better developed than the longitudinal fibres, which are delicate and often difficult to determine in transverse sections. They are arranged internally to the circular layer in the anterior part of the ileum, but towards its distal extremity some of the fibres seem to migrate to the outer surface of the circular muscle-layer.

Colon.—There is no marked difference at first between this region and the one immediately preceding it. The epithelium (Pl. III. fig. 21) is thrown into large longitudinal folds which almost completely fill the lumen. The cells are large and the cytoplasm is not differentiated into two regions as it is in the ileum. With the apposition of the Malpighian tubes on the walls of the distal part of the colon the cells (Pl. III. fig. 22) gradually decrease, the longitudinal folds disappear, and the muscle-layers become progressively weaker until, in the distended portion, in which the Malpighian tubes form a ramifying system beneath the peritoneal membrane, the component parts of its walls can only be distinguished with difficulty. The chitinous intima is not strongly developed in the colon.

The walls of the *rectum* (Pl. III. fig. 23) consist of essentially the same layers as are present in the colon. The lumen, however, is smaller, on account of the presence of a variable number of longitudinal folds of the epithelium and intima. The cells are small and somewhat ill defined, and the narrow intima is continuous distally with the cuticle. New and strongly developed circular muscles (*c.m.*) make their appearance at the commencement of the rectum. There are usually two layers of these muscles arranged in regular annular bands, which encircle the epithelium and give to the wall of the rectum a more or less corrugated appearance.

Malpighian Tubes.

The six Malpighian tubes arise separately at the distal end of the mesenteron, immediately anterior to its junction with the ileum. They are continuous with the epithelium of the mesenteron, but, as is seen in a slightly tangential transverse section through this region (Pl. III. fig. 19), very few mesenteron cells intervene between the origin of the Malpighian tubes and the beginning of the ileum. The six tubes are morphologically divisible into two series which unite at their distal ends to form a ramifying system on the outer wall of the colon.

The first series (*Mt.*$_1$, text-figs. 6 & 7) comprises a dorsal and a ventral pair of long, relatively wide, brownish vessels, which pursue a very tortuous and convoluted course throughout the body-cavity. They are held in position on the dorsal and ventral walls of the large proximal part of the mesenteron by numerous tracheæ, but lie embedded in the fat-body distally. They pass anteriorly as far as the crop, and then, reversing their course, extend backwards to the seventh or eighth abdominal segment. Thence they redouble upon themselves as far as the fifth or sixth segment, where the dorsal and ventral vessels of each side coalesce to form a single tube (*sm.*$_1$, text-fig. 7).

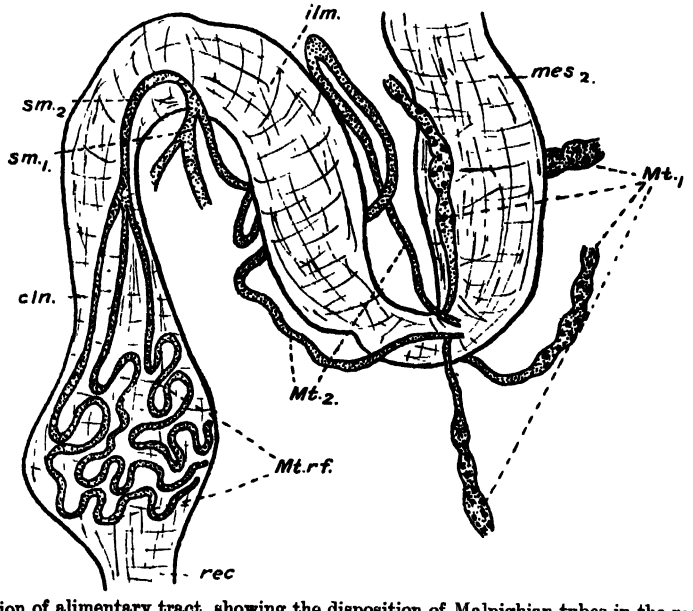
The second series (*Mt.*$_2$, text-fig. 7) consists of a pair of narrow milky-white tubes arising just anterior to, and between the origins of, the first series. They follow the course of the ileum, and may have one or two slight convolutions, but on the whole they are relatively straight. The vessel of each side unites with the single tube of the first series to form a common stem or trunk (*sm.*$_2$). The two common stems which are thus formed by the union of three Malpighian tubules on each side become closely associated with the wall of the colon. They run parallel with the colon for a short distance, and then each divides into three

separate vessels which ramify over the wall of the colon in the seventh and eighth abdominal segments (*Mt.rf.*, text-fig. 7). In this region the peritoneal layer of each Malpighian tube coalesces with that of adjacent tubes to form two continuous sheaths which enclose the six Malpighian vessels. The inner sheath becomes closely apposed to the wall of the colon, with which, however, the Malpighian tubes do not communicate, each ending blindly at the beginning of the rectum.

A somewhat similar disposition of the Malpighian tubes obtains in most Chrysomelid and many other coleopterous larvæ (Dufour, 1843; Metalnikov, 1908; Poyarkoff, 1910; van Gorka, 1914; and Woods, 1916).

Valéry Mayet (1896), Vaney (1900), and Sinety (1900) describe the occurrence of two series of Malpighian tubes in other forms of insects, and suggest that, while the long yellowish or brownish tubes are clearly renal in function, the white tubes may be either partially or completely modified for the reservation of calcium

Text-figure 7.



Portion of alimentary tract, showing the disposition of Malpighian tubes in the region of the colon, × 40.

carbonate. Keilin (1921) has also demonstrated the presence of $CaCO_3$ in the Malpighian tubes and fat-body of many dipterous larvæ.

There is little histological difference between the vessels of the two series of tubes. The tubes of the first series have large cells which contain numerous golden-brown concretions, while the cells in the second series are smaller and have few concretions. In transverse section the tube is seen to consist of three or four cells, each of which has a conspicuous, rounded, basal nucleus. The cytoplasm towards the narrow lumen stains less deeply than that at the base of the cell. It often exhibits faint striations, and frequently a vacuolated condition is noticeable. The cells are supported by a delicate basement-membrane, external to which there is a narrow, nucleated, peritoneal layer (*pn.m.*, Pl. III. fig. 21). The cells and nuclei of the tubes, which are in apposition to the walls of the colon, are comparatively small, and the lumen of the tube is also reduced.

Nephrocytes.

In connection with the process of excretion most insects have several groups of nephrocytes, which are usually located dorsally in the pericardial sinus. Keilin (1917) and Puri (1925) have shown that in dipterous larvæ a ventral peri-œsophageal group is also present, while in *Pediculus*, according to Nuttall and Keilin (1921), the dorsal nephrocytes are scattered throughout the fat-body. Injection experiments, as described by Nuttall and Keilin, were performed on larvæ of *Paraphædon*. Ammonia-carmine was injected into the posterior region of the body-cavity by means of very fine pipettes, and after a variable number of hours the larvæ were dissected and examined for nephrocytes. In some larvæ a few cells in the dorsal part of the perivisceral fat-body appeared to be coloured red, but in most of them no nephrocytic cells could be distinguished.

In transverse sections of the larvæ (Pl. III. fig. 24) there are deeply staining cells situated on either side of the dorsal vessel (*ht.*). These cells (*p.c.*) are frequently mononuclear, and are easily distinguished from the adjacent fat-body cells (*f.b.*) by their less vacuolated cytoplasm. Two small bodies (*n.b.*), probably nucleoli, are present, and occasionally a binucleate condition is exhibited. These cells may be analogous with the pericardial nephrocytic cells observed by Kowalevsky (1889), Imms (1908), Bruntz (1908, 1909), and Keilin (1917) in various larval insects, in most of which the cells are either binucleate or multinucleate.

Puri (1925) has described uninucleate cells on either side of the anterior part of the aorta in *Simulium*, but he considers that they are not nephrocytic in function. Although an excretory function has not been demonstrated in the cells on either side of the dorsal vessel in *Paraphædon*, it is probable that they are comparable with the pericardial nephrocytic cells described by Poyarkoff (1910) in the closely related larval form of *Galerucella*.

Circulatory System.

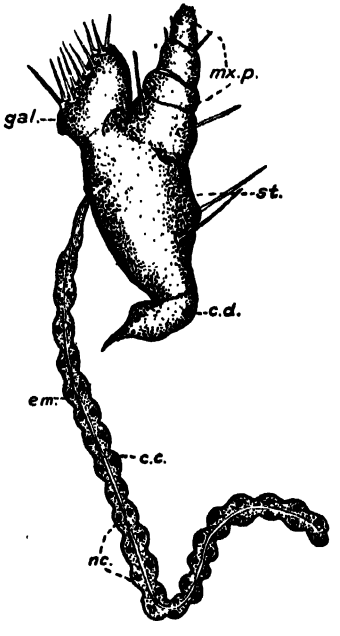
The dorsal vessel is an extremely narrow tube lying mid dorsally below the integument. It extends from the eighth abdominal segment to the head, where it ends in a funnel-shaped aperture at the base of the brain. The proximal portion lying in the thoracic segments is the aorta, while the slightly dilated abdominal portion is the heart, which is supported in each segment by paired alary muscles (*a.m.*, Pl. III. fig. 24). The alary muscles are attached near the proximal border of each tergite, and are spread out fan-wise, the muscles of each pair uniting below the heart. The heart does not seem to be divided into chambers, as no ostia were observed. Payne (1916) was also unable to find ostia in the heart of *Telephorus*. The heart has the appearance of a delicate continuous muscular tube, which may be slightly dilated in each abdominal segment. Its walls are very thin and the cells are greatly flattened. The nuclei (*nc.*, Pl. III. fig. 24) are arranged opposite each other and project laterally into the lumen of the heart.

Maxillary Glands.

In the larva of *Paraphædon* there are no glandular appendages associated with the alimentary canal, as gastric cæca and salivary glands are undeveloped. Many insects which lack salivary glands are provided with other secretory organs, which usually open at the bases of the mandibles. In *Paraphædon* similar secretory organs open on to the dorsal surface of the galea of the maxilla. These maxillary glands (text-fig. 8) are long and slender, and are situated in the prothorax on either side of the subœsophageal and prothoracic ganglia. They are very simple in structure, consisting of a central chitinous canal (*c.c.*) surrounded by an epithelial layer (*em.*) of large cells. The cytoplasm is granular, and the nuclei (*nc.*) are relatively large. The cells decrease in size towards the proximal extremity of

the gland, and the chitinous canal becomes continuous with the cuticular surface of the galea. The distal extremity of the gland ends blindly in the lateral part of the

Text-figure 8.



Right maxilla and maxillary gland of third-stage larva, × 100.

prothorax. Poyarkoff (1910) describes similar organs in the larva of *Galerucella*, and refers to them as salivary glands.

Muscular System.

The early researches of Lyonet (1762) and Lubbock (1858), and the more recent investigations of Forbes (1914) on the musculature of lepidopterous larvæ have shown that, even in the larval stage of insects, in which the muscular system exhibits its least modified condition, the arrangement of the muscles is very complicated. A systematic account of the muscular system of insects has not yet been published, and, as the homologies of some of the muscles are somewhat obscure, a uniform nomenclature has not evolved from the detailed studies which have been undertaken. The general arrangement of the principal muscles, however, does not appear to vary greatly, and the terminology used by Du Porte (1920), rather than that of Bauer (1910), may be applied to the muscles in *Paraphædon*.

The muscles are thought to be inserted on the cuticle by means of "tonofibrille" cells similar to those described by Poyarkoff (1910) in the larva of *Galerucella*.

A. *Muscles of the Head.*

Most of the muscles attached to the head-capsule are concerned with the movements of the mouth-parts and antennæ.

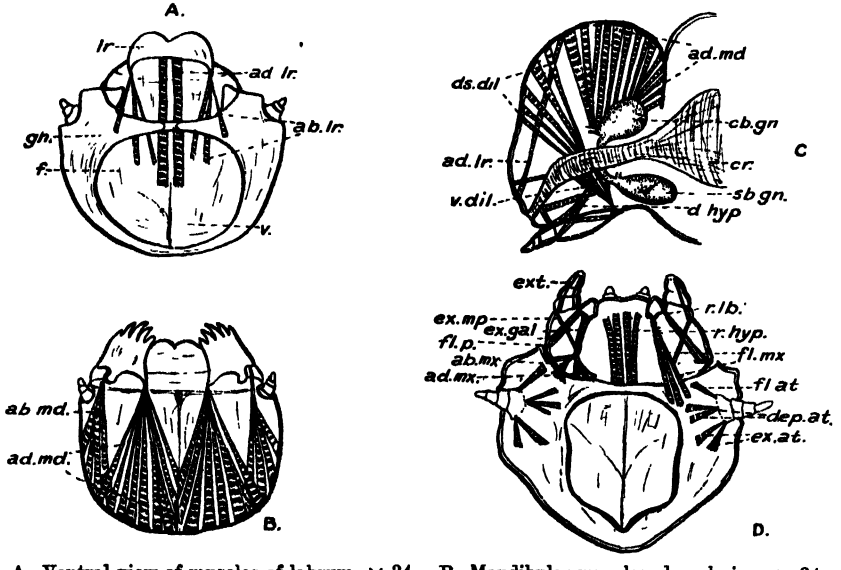
Labrum.—There are two sets of muscles controlling the movements of the labrum. The ***abductors*** (*ab.lr.*, text-fig. 9, A) consist of a pair of broad contiguous

muscles, arising in the distal part of the frons, and having their insertion at the base of the labrum on either side of the median line. The *adductors* (*ad.lr.*, text-fig. 9, A) comprise two or three slender fibres which are attached to the head-capsule, laterally to the origin of the abductors. They are inserted at the base of the labrum near its lateral border.

Mandibles.—The muscles associated with the mandibles occupy the greater part of the head-cavity and are divided into two principal sets. The *adductor* muscle (*ad.md.*, text-fig. 9, B) is the larger, and the points of attachment of its numerous fibres cover most of the dorsal surface of the head-capsule. It is inserted into the inner basal angle of the mandible by a broad flat tendon. The *abductor* (*ab.md.*, text-fig. 9, B) is a smaller muscle inserted into the outer angle of the mandible. It arises in the lateral wall of the head-capsule.

Maxillæ.—The disposition of the maxillary muscles (text-fig. 9, D) is more

Text-figure 9.



A. Ventral view of muscles of labrum, × 34. B. Mandibular muscles, dorsal view, × 34. C. Side view of cephalic muscles, × 40. D. Muscles of head appendages, ventral view, × 40.

complicated than that of other head-appendages owing to the segmented condition of its parts. The *adductors* of the maxilla (*ad.mx.*) arise as a pair of short broad muscles on the tentorium, and pass to the postero-lateral border of the cardo. A short *abductor* muscle (*ab.mx.*) arises anteriorly on the gena, and is attached to the distal margin of the cardo, near the insertion of the adductors. A strong compound muscle of three fibres (*fl.mx.*) originates at the anterior end of the gena, and runs to an insertion by a slender tendon at the inner base of the galea. It is believed to be comparable with the *flexor muscle* of the maxilla in *Gryllus* (Du Porte, 1920), as, working in conjunction with the adductors of the maxilla, it serves to close this appendage. The *extensor of the galea* (*ex.gal.*) is a slender muscle inserted at the outer basal angle of the galea, and arising at the inner basal angle of the stipes. The extensor muscle of the maxillary palpus (*ex.mp.*) is dorsal to the flexor muscle of the palpus (*fl.p.*). The former arises at the inner proximal angle of the stipes, and is inserted at the outer lateral base of the palpus.

The flexor is a double muscle running from the outer lateral wall of the stipes to the inner base of the palpus. Within the joints of the palpus there are outer extensor (*ext.*) and inner flexor (*fl.*) muscles.

Labium.—The musculature of the labium is very simple. There is a pair of broad, almost contiguous, *retractor* muscles (*r.lb.*, text-fig. 9, D), which originate on the tentorium and are inserted one on each side of the ligula. There may be short extensor and flexor muscles within the joints of the palpi.

Hypopharynx.—A pair of flat *retractor* muscles (*r.hyp.*, text-fig. 9, D) runs parallel and dorsal to the retractors of the labium. They arise on the tentorium close to the latter muscles and are inserted anteriorly in the ill-defined region at the junction of the labium and hypopharynx. Originating from the lateral bar of the hypopharynx there is a short *compressor* muscle which runs obliquely inwards, and is inserted with its fellow of the opposite side near the median line at the junction of the hypopharynx and labium. There seems to be a *depressor* muscle (*d.hyp.*, text-fig 9, C) arising in the submentum and running to the distal part of the hypopharynx, near its junction with the œsophagus.

Muscles of the Antennæ.—The antennæ are provided with at least three sets of muscles (text-fig. 9, D). The extension of the antenna is effected by a double muscle (*ex.at.*) inserted distally into the base of the first joint. It seems to arise posteriorly on the gena. The *flexor* (*fl.at.*) is a single muscle arising on the frons, and is inserted into the proximal side of the first antennal joint. Several *depressor* muscles (*dep.at.*) arise on the tentorium, and are attached to the ventral base of the antenna.

Muscles of the Pharynx.—A series of paired muscles arises, one behind the other, on the frons, and is inserted on either side of the mid-dorsal wall of the pharynx in front of the brain. There are three or four anterior muscles (*ds.dil.*, text-fig. 9, C), and three broader posterior muscles. By their contraction they serve to raise the dorsal wall of the pharynx, and they are therefore *dilator* muscles. There are six or seven slender *ventral dilators* (*v.dil.*, text-fig. 9, C) originating in the dorso-lateral angle of the tentorium. They are inserted into the ventro-lateral wall of the pharynx, distal to the insertion of the dorsal dilators.

Muscles controlling the Movements of the Head.

Du Porte (1920) has classified the muscles which direct the movements of the head into depressors, elevators, retractors, and rotators. In *Paraphædon* the muscles associated with the movements of the head (text-fig. 10) arise in the prothorax, and are inserted at various points along the occipital foramen and tentorium. The following muscles may be distinguished:—

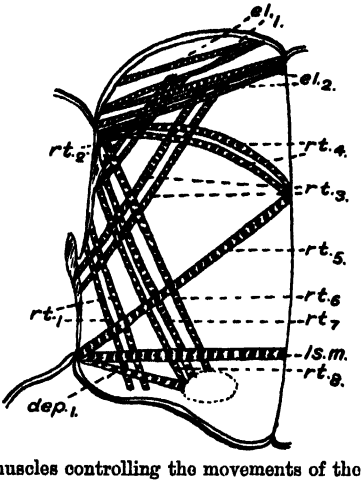
(a) *Sternal.*—There is a broad ventral depressor muscle (*dep.*, text-fig. 10) which arises in front of the base of the leg. It is inserted into the distal border of the tentorium near the insertions of the prothoracic longitudinal muscles, which no doubt act as additional depressor or retractor muscles of the head. A pair of slender muscles ($rt._1$) originates in the sternite anterior to the depressor muscle and is inserted into the lateral border of the occipital foramen. They serve as rotator muscles of the head.

(b) *Tergal.*—The dorsal system of elevator muscles comprises two pairs of longitudinal muscles which arise on the posterior margin of the prothorax. The first pair ($el._1$) is inserted mid-dorsally into the intersegmental region between the cranium and the pronotum. The second pair ($el._2$) arises laterally to the first pair, and is inserted mid-dorsally on the cranium. In addition to these several weak muscles run obliquely from the origin of $el._1$ to the insertion of $el._2$. They possibly assist in the rotation of the head. A pair of short rotators ($rt._2$) arises mid-dorsally on the pronotum and is attached to a lateral apodeme on the occipital

foramen. Another pair of rotators ($rt._3$) originates laterally to the preceding pair and is inserted laterally on the tentorium.

(c) *Pleural.*—A pair of relatively strong fibres ($rt._4$) arises in the pleural region on the posterior margin of the prothorax. It passes obliquely upwards and forwards to the mid-dorsal border of the occipital foramen. These muscles are comparable with the pleural diagonal muscles in other segments, and serve as

Text-figure 10.



Prothoracic muscles controlling the movements of the head, × 40.

rotator muscles of the head. Another strong rotator ($rt._5$) arises with $rt._4$, but is inserted ventrally on the tentorium. The prothoracic diagonal sterno-pleural (*P.dg.*, text-fig. 11, A) muscle, which arises on the posterior margin of the prothorax, and is inserted on the tentorium, is also a strong rotator muscle.

(d) *Tergo-sternal.*—Three oblique fibres ($rt._6$, $rt._7$, $rt._8$) arise at the base of the leg and are inserted dorso-laterally on the head-capsule.

B. *Muscles of the Thorax.*

1. *Prothorax.*

Several muscles may be absent in the prothorax, while many of them are modified in correlation with their proximity to and association with the head. In addition to those directly functioning in the movements of the head, there are other prothoracic muscles which are homologous with those of the meso- and metathorax. These include four broad *longitudinal sternal* (*ls.m.*, text-fig. 11, A) and several *dorso-ventral* muscles. The latter comprise a *tergo-sternal* intersegmental muscle (*P.ts.*), two pairs of anterior (*an.p.*), and two pairs of posterior (*pn.p.*) *noto-pedal* muscles, which apparently correspond with certain of the noto-subcoxals and noto-coxals in *Gryllus* (Du Porte), as they extend between the pronotum and the sclerites at the base of the leg. In *Paraphædon* the noto-pedal muscles in the proximal half of the thoracic segments are inserted on the margins of the triangular sclerite (*tb.*XI.) anterior to the coxa, while those in the posterior half are attached immediately behind tubercle XII. at the base of the leg. They effect the backward and forward movements of the leg, and have been termed flexor and extensor muscles respectively by Du Porte (1920).

In the prothorax there is one *pleuro-pedal* muscle (*pd.m.*) which arises intersegmentally and passes to the sternite, distal to the base of the leg.

2. *Mesothorax and Metathorax.*

In the mesothorax and metathorax (text-fig. 11, A) the anterior and posterior noto-pedal muscles are disposed similarly to those of the prothorax. There are, however, three instead of four posterior noto-pedal muscles in the two former segments. In addition to these, the following groups of muscles may be noted:—

(a) *Sternal Muscles.*—There are five broad longitudinal sternals (*ls.m.*) on each side of the nerve-cord. Oblique sterno-pedal (*spd.*) muscles arise mid-ventrally and are inserted near the outer bases of the legs. In addition to these there are diagonal sternal muscles (*dg.s.*) which arise mid-ventrally in the intersegmental region, and pass outwards to the insertion of the longitudinal sternal muscles.

(b) The *sterno-pleural* muscles comprise a relatively broad fibre, which is situated in the distal part of the segment, and two slender muscles (*s.pl.*$_2$) which are inserted on the anterior subspiracular tubercle (*tb.*1X.). The former single muscle (*s.pl.*$_1$) arises intersegmentally, and passes obliquely forwards to the posterior subspiracular tubercle (*tb.*X.). In the mesothorax the two proximal sterno-pleural muscles supply the levers of the closing apparatus of the spiracle. There is also a relatively broad, diagonal, sterno-pleural muscle (*sp.l.*$_3$).

(c) A pair of *pleuro-pedal* muscles (*pd.m.*) arises posteriorly in the subspiracular region and is inserted near the posterior tubercle at the base of the leg. A similar pair of muscles is present in the prothoracic segment, but they are inserted dorso-laterally on the pronotum. There may be an extra pleuro-pedal muscle (*pd.m.*$_2$) in the anterior half of the segment. It passes forwards from the anterior sclerite at the base of the leg to the intersegmental insertion of the longitudinal pleural muscles of the mesothorax.

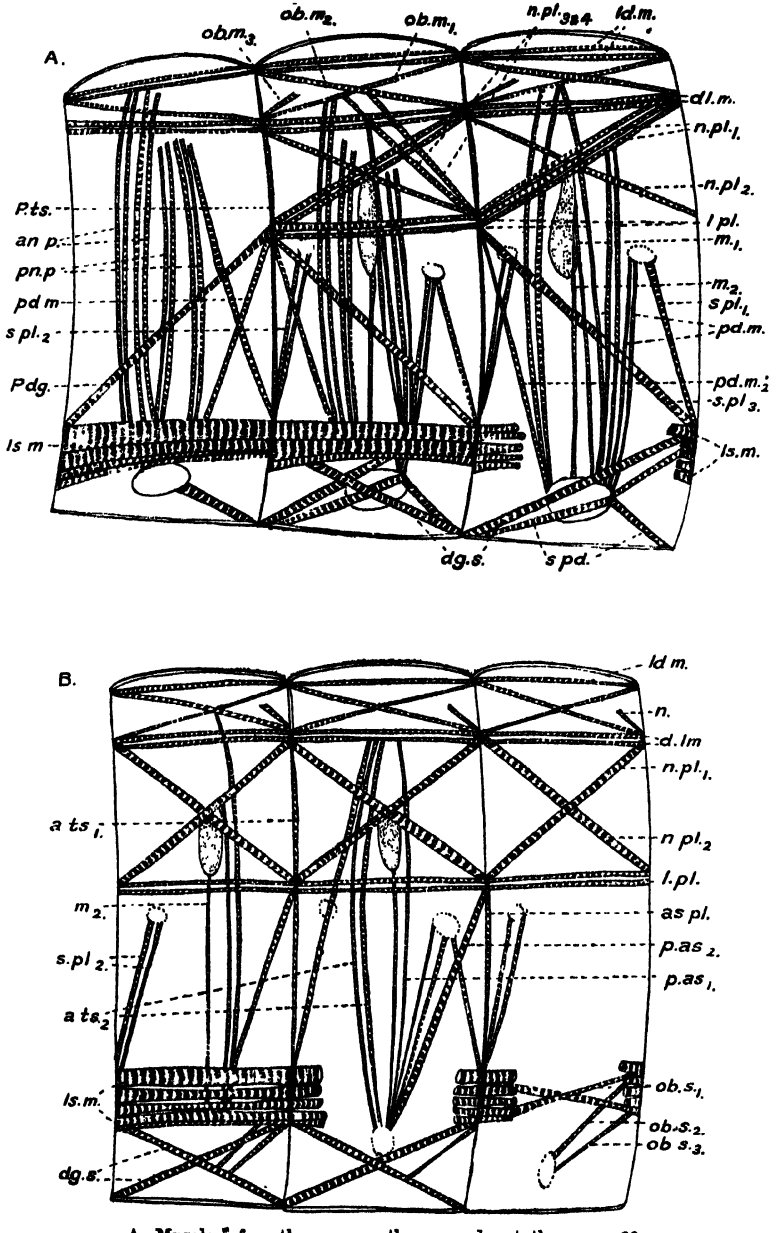
(d) *Noto-pleural.*—Ventral to the reservoir of the eversible glands there is a system of diagonal muscles which, in the mesothorax, extends between a pair of *longitudinal pleural* muscles (*l.pl.*) and the pair of *dorso-lateral* longitudinal muscles (*dl.m.*). In the metathorax the longitudinal pleural muscles are absent, but three broad *noto-pleural* muscles (*n.pl.*$_1$) are developed. Dorsal to these there is a single noto-pleural muscle (*n.pl.*$_2$) which passes obliquely outwards from the dorso-lateral to the longitudinal pleural muscles, intersecting the first series of noto-pleurals ventro-laterally to the base of the eversible glands. In the posterior half of the mesothorax there are two shorter noto-pleural muscles (*n.pl.*$_3$, *n.pl.*$_4$).

(e) The *dorsal longitudinal* muscles are arranged similarly to those of the prothorax, into mid-dorsal longitudinals (*ld.m.*) on either side of the dorsal vessel and a pair of slender dorso-lateral longitudinal muscles (*dl.m.*). Passing backwards and inwards (mid-dorsally) from the dorso-laterals to the mid-dorsal muscles there is an oblique muscle (*ob.m.*$_1$), which seems to be absent in the prothorax. A second muscle (*ob.m.*$_2$) runs obliquely outwards from the anterior margin of the segment, and lies dorsal to the first oblique. It is comparable with the oblique dorsal muscle in the prothorax. In addition to these there is a short oblique notal muscle (*ob.m.*$_3$) lying in the anterior half of the meso- and metathoracic segments. The large eversible glands are controlled by three delicate muscles. The anterior muscle seems to originate on the dorso-lateral margin of the anterior subspiracular tubercle, while the median muscle (*m.*$_2$, text-figs. 5 & 11, A), which is inserted at the base of the reservoir, arises on the posterior border of the anterior pleural tubercle (XI.) at the base of the leg. The posterior muscle (*m.*$_1$) is attached with other transverse muscles near the posterior pleural tubercle (XII.), and is inserted at the base of the atrium of the eversible process. These muscles lie embedded in the fat-body, ventro-laterally to the noto-pedal muscles.

C. *Muscles of the Abdomen.*

Although relatively fewer muscles are developed in the abdomen, the musculature is essentially similar to that of the thorax. The following slight differences may, however, be noted.

Text-figure 11.



A. Muscles of prothorax, mesothorax, and metathorax, × 60.

B. Muscles of anterior abdominal segments, × 60.

In addition to the well-developed longitudinal (*ls.m.*, text-fig. 11, B) and diagonal *sternal* muscles (*dg.s.*), there are three oblique sternals (*ob.s.*$_{1,2,\&3}$) lying ventrally to the longitudinal sternals. The posterior *sterno-pleural* muscle of the thoracic segments seems to be absent in abdominal segments, but another sterno-pleural (*as.pl.*), not observed in the thorax, lies below the intersegmental tergo-sternal muscle (*at.s.*$_1$).

In each abdominal segment there is one pair of anterior (*a.ts.*$_2$), and only a single posterior (*p.as.*$_1$), *tergo-sternal* muscle, which are respectively homologous with the paired anterior and posterior noto-pedal muscles in the meso- and metathorax. They originate on the sternum close to the ventro-lateral tubercle, and are inserted on the mesial margin of the posterior dorsal tubercle In the posterior half of the segment there is also a relatively broad *sterno-pleural* muscle (*p.as.*$_2$), which is comparable with the pleuro-pedal muscle in the prothorax.

Longitudinal *pleural* muscles (*lp.l.*) are segmentally arranged in the abdomen, but otherwise are only present in the mesothorax. The *noto pleural* muscles are less numerous in abdominal segments, but the disposition of the single diagonal muscles (*n.pl.*$_{1\&2}$) is similar to the arrangement of the homologous thoracic muscles. In the posterior half of each abdominal segment there is a very short oblique *notal* muscle (*n.*), which is unrepresented in the thorax. On the other hand, the anterior oblique notals (*ob.m.*$_3$) of the thorax are absent in abdominal segments.

The segmental arrangement of the muscles is constant for abdominal segments 1 to 7. In the eighth segment the posterior sterno-pleural (*s.pl.*) of other segments is lacking, but the remaining muscles are relatively well developed. In the ninth segment there are a few very delicate transverse muscles, the homologies of which are not clear. The longitudinal, tergal, and sternal muscles converge towards the rectum in the ninth segment, and are inserted on the body-wall of the anal proleg. They are probably instrumental in effecting certain of the movements of the anal region.

D. *Muscles of the Legs.*

The muscles of the leg (text-fig. 12) are broader and flatter than most of the body-muscles, which, with the exception of the sternals and noto pleurals, are somewhat cylindrical. The muscles lying within the leg consist of extensors and flexors, and may be considered separately in each joint.

(a) *Pleuro-coxal.*—Three short broad muscles (*ex.cx.*) are spread out fanwise over the anterior tubercle (XI.) at the base of the leg. They arise on the dorsal border of the tubercle and are inserted on the antero dorsal margin of the coxal opening. They act as extensors of the coxa, and move the leg in a forward and upward direction.

(b) *Coxo-trochanteric.*- Three extensor muscles of the femur (*ex.fem.*$_{1,2,\&3}$) arise on the postero-dorsal margin of the coxa, and are inserted on the anterior face of the trochanter. A fourth extensor muscle (*ex.fem.*$_4$) originates antero-dorsally on the coxal opening and is inserted similarly on the trochanter. The flexor muscles of the femur lie on the ventral side of the leg. They comprise two anterior (*fl.fem.*$_{1\&2}$) and one posterior (*fl.fem.*$_3$) flexor.

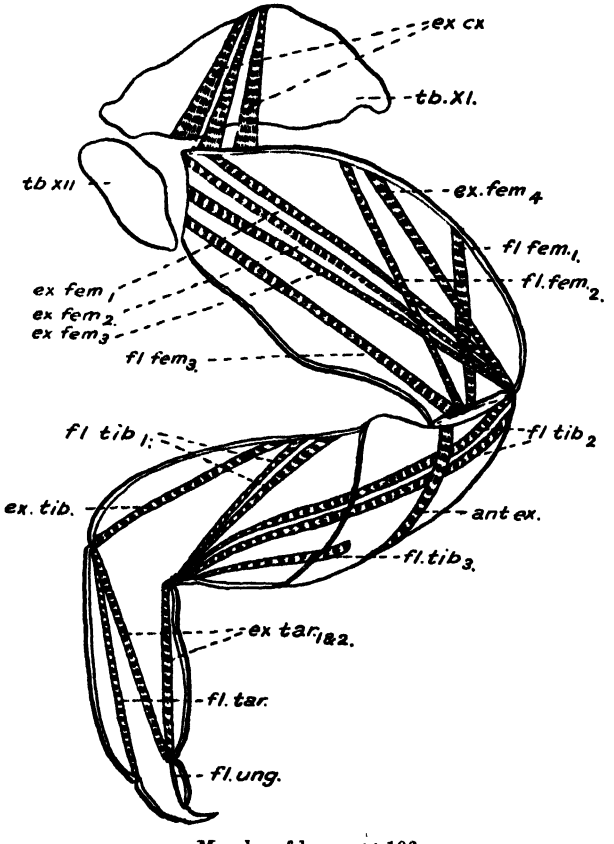
(c) *Trochantero-femoral.*—A short muscle (*ant.ex.*) appears to run from the proximal margin of the trochanter to the anterior face of the femur and acts as an extensor of the femur.

(d) *Femoro-tibial.*—There is a single extensor of the tibia (*ex.tib.*), which arises from the proximal end of the femur and is inserted on the dorsal side of the postero-lateral margin of the tibia. There is a pair of dorsal flexors (*fl.tib.*$_1$) inserted antero-dorsally on the tibia, and two sets of ventral flexors (*fl.tib.*$_{2\&3}$).

(e) *Tibio-tarsal.*—The flexor of the tarsus (*fl.tar.*) is a single muscle inserted on

the postero-lateral margin of the tarsus. There are also two extensor muscles (*ex.tar.*$_{1\&2}$) which lie in the dorsal part of the leg and are inserted anteriorly on the tarsus.

Text-figure 12.



Muscles of legs. × 106.

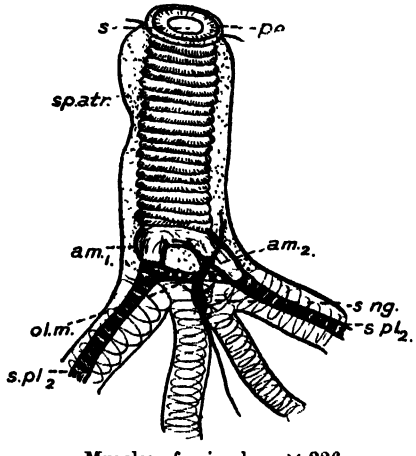
(*f*) *Tarsal.*—The tarsus is reduced to a single segment, which terminates in a curved claw. There seems to be only a single flexor (*fl.ung.*), and no extensor muscle in the tarsus.

E. *Muscles of the Spiracles.*

The spiracles in the two regions of the body differ principally in their relative sizes, those of the mesothorax being considerably larger than those of the abdomen. They are very simply constructed and may be classified under the *Spiracula uniforia* of Steinke (1919). The annular peritreme (*pe.*, text-fig. 13) is slightly raised above the surface of the body, and supports a delicate transparent membrane which extends between the peritreme and the small spiracular opening (*s.*, text-fig. 13). The latter leads into a short tubular atrium (*sp.atr.*), the walls of which are greatly reinforced by annular thickenings and are provided with numerous short stiff hairs or ctenidia. There are also stronger hairs projecting

from the peritreme towards the stigma. The last annular thickening at the base of the atrium is modified to form the closing apparatus of the spiracle. The strong chitinization of the basal ring is incomplete ventrally, but lateral prolongations project from the semicircular dorsal band. The anterior prolongation or lever (*am.*$_1$, text-fig. 13) is short and rounded, while the posterior (*am.*$_2$) is very conspicuous. They serve as the attachments of the anterior sterno-pleural muscles (*s.pl.*$_2$, text-fig. 11, A & B, & text-fig. 13), which, by their contraction, pull the two

Text-figure 13.



Muscles of spiracle. × 226.

levers apart and open the entrance into the tracheæ communicating with the atrium. They are therefore the dilator muscles of the spiracle. Between the two levers there is a short broad occlusor muscle (*ol.m.*) which, upon contraction, closes the entrance into the tracheæ by bringing the two levers, and, consequently, the walls of the atrium, together. At the base of the occlusor muscle there is a fairly conspicuous nerve-ganglion (*s.ng.*) which probably belongs to the ventral sympathetic nervous system.

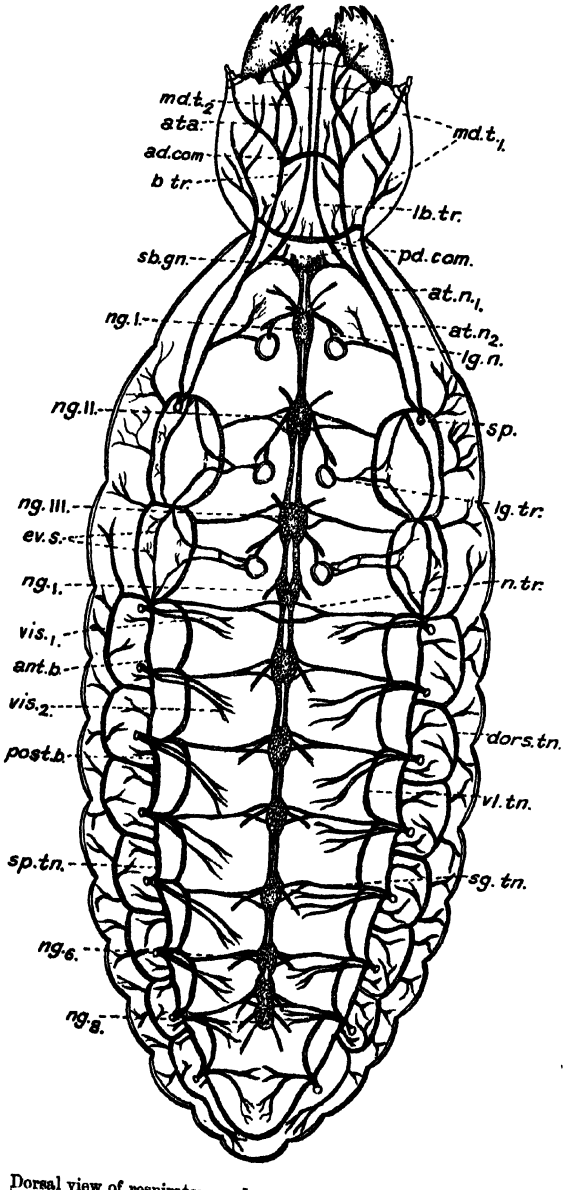
Respiratory System.

The tracheal system (text-fig. 14), like most of the other systems in the larva, is bilaterally symmetrical and segmentally arranged. The spiracles (*sp.*) are disposed laterally in the mesothoracic and first eight abdominal segments. In each segment the atrium of the spiracle communicates directly with a rather intricate system of branching tracheæ, some of which anastomose to form longitudinal tracheal trunks, while others proceed immediately to the various organs in the body-cavity.

Abdominal Tracheæ.

In each abdominal segment five tracheal branches diverge from the base of the atrium. Two of these, the visceral tracheæ (*vis.*$_1$ & $_2$), run parallel to each other transversely across the anterior half of the segment. One supplies the dorsal wall and the other the ventral wall of the alimentary tract. They are very well developed in the first four abdominal segments, in which they serve to maintain the vessels of the first series of Malpighian tubes in position on the dorsal and

Text-figure 14.



Dorsal view of respiratory and ventral nervous systems. × 35.

ventral walls of the proximal division of the mesenteron. Ventral to these an anterior (*ant.b.*) and a posterior trachea (*post.b.*) are given off at the base of the atrium. These unite respectively with the posterior and anterior branches of adjacent segments to form a continuous longitudinal spiracular trunk (*sp.tn*) which lies in the pleural region, and not only supplies the fat-body, but also sends a very delicate trachea (*ev.s.*) to each eversible segmental process. At the posterior end of the body the two spiracular trunks unite dorsally to the rectum, to the walls of which they give off fine tracheal branches.

A delicate dorsal longitudinal trunk (*dors.tn.*) is formed by the anastomosis of dichotomizing branches arising in the middle of each segment from the spiracular trunk. Tracheæ from this dorsal trunk supply the dorsal fat-body and alary muscles of the heart. The remaining tracheal branch originating at the base of the atrium lies below the two visceral tracheæ in the anterior half of the segment. It runs towards the mid-ventral line for some distance and then bifurcates. The branches so formed unite with those of adjoining segments, constituting a continuous, somewhat curved, ventro-lateral tracheal trunk (*vl.tn.*). Segmental tracheæ are given off from this trunk into the fat-body, and in the anterior part of each segment a fairly stout trachea (*sg.tn.*) proceeds transversely across the segment and anastomoses with that of the opposite side below the nerve-cord. From this ventral commissure a short trachea (*n.tr.*) is given off anteriorly on each side to the nerve-ganglion.

Thoracic Tracheæ.

The spiracular and ventro-lateral tracheal trunks are continued into the thorax, but the dorsal trunk ceases in the anterior half of the first abdominal segment. Tracheæ arising from the spiracular trunk supply the fat-body and dorsal vessel in the meso- and metathoracic segments. The tracheæ to the meso- and metathoracic eversible glands and legs (*lg.tr.*) arise primarily from the tracheal branch, which later bifurcates and forms the ventral trunk in these two segments. A certain amount of anastomosis occurs, however, at the bases of the glands and legs before the respective tracheæ are given off. The ventral commissures in the meso- and metathorax are formed as in abdominal segments, but the trachea to the nerve-ganglion is directed posteriorly, and not anteriorly, as it is in the latter segments. The ventral trunk is not continued into the prothorax, in which segment the legs and the prothoracic and subœsophageal ganglia are supplied by tracheæ from the principal trunk proceeding to the head.

Cephalic Tracheæ.

Two anterior tracheal trunks diverge from the mesothoracic spiracle on each side, and, proceeding through the prothorax, enter the head. The outer (dorso-lateral) of these ($atn._1$) subdivides into numerous branches ($md.t._1$) which supply the mandibular muscles. It also gives off a dorsal trachea which unites with the corresponding trachea of the opposite side to form a dorsal commissure (*pd.com.*) around the occipital foramen. The inner and stouter trunk ($atn._2$) from the mesothoracic spiracle supplies most of the head-appendages and organs of its side. At the antero-ventral border of the prothorax a delicate trachea (*lb.tr.*) is given off, and, passing beneath the tentorium, it runs to the labium and maxillæ. On entering the head the main trunk gives rise to a short trachea (*b.tr.*) to the brain, and in front of the brain it divides into three important tracheæ. The outer of these (*atn.*) passes laterally to the antenna and also sends a branch ventrally to the mesial margin of the mandible. The second trachea ($md.t._2$) chiefly supplies the mandible, while the third unites with its fellow of the opposite side to form an anterior dorsal commissure (*ad.com.*). from which branches may be given off to the labrum.

Nervous System.

The *central nervous system* (text-fig. 14, & Pl. IV. figs. 25–26) comprises a brain, a subœsophageal ganglion, and a series of eleven segmentally-arranged ventral ganglia, which are united to each other by paired longitudinal connectives, indicating the originally double nature of the ventral nerve-cord.

The *brain* (*cb.gn.*) consists of a pair of cerebral or supra-œsophageal ganglia, situated within the head above the œsophagus. The two ganglia are closely approximated, and the communicating transverse commissure is inconspicuous. The three primary divisions constituting the brain of orthopterous insects are not differentiated in the larva of *Paraphœdon*, but the slightly enlarged roots of the optic, the antennary and the labral nerves, may represent the protocerebral, deutocerebral, and tritocerebral lobes respectively. Each cerebral ganglion gives off four antero-lateral nerves. The *optic nerve* (*o.n.*, Pl. IV. figs. 25–26) arises dorsally, and, passing forwards and outwards, it divides into short ocellar nerves which innervate the ocelli. The *antennary nerve* (*ap.n.*) lies immediately below the optic nerve and runs parallel with it for most of its course. It does not divide before entering the antenna. A somewhat stronger *labro-frontal nerve* (*lf.n*) emerges ventro-laterally from the supra-œsophageal ganglion and, passing round the dorsal dilator muscles of the pharynx, it meets the corresponding nerve of the opposite side in the frontal ganglion (*f.gn.*) of the visceral nervous system. Beneath, and almost contiguous with the labro-frontal nerve, a delicate *labral nerve* (*lr.n.*$_1$) passes forwards to the labrum. There is a very fine connecting nerve between the labral nerve and the postœsophageal commissure. Arising from the antero-ventral border of the brain there is a narrow *post-œsophageal commissure* (*pt.com.*) which passes around the œsophagus and connects the two tritocerebral lobes. Each cerebral ganglion is connected with the subœsophageal ganglion by means of a broad *para-œsophageal connective* (*pa.ct.*, Pl. IV. fig. 26), from which a delicate ganglionated nerve passes forwards parallel to the œsophagus, and appears to innervate the hypopharynx.

The *subœsophageal ganglion* (*sb.gn.*) is situated near the anterior margin of the prothorax below the tentorium. It gives off paired nerves which innervate the mouth-parts. The *mandibular nerve* (*md.n.*) arises antero-ventrally to the para-œsophageal connective on each side and runs parallel to the œsophagus for some distance before dividing into branches which supply the mandibular muscles. The roots of the two remaining nerves are situated postero-laterally to the para-œsophageal connectives. The *maxillary nerve* (*mx.n.*) is directed forwards and outwards to supply the maxillary palpus. The *labial nerve* (*lb.n.*) passes directly to the labium, below the maxillary nerve.

Ventral Nerve-cord.—The nerve-cord consists of three thoracic (*n.g.* I., II., and III., text-fig. 14) and eight abdominal ganglia (*ng.*$_{1-8}$). The three thoracic ganglia are situated in the middle of their respective segments, but the abdominal ganglia are arranged more or less intersegmentally, each ganglion lying proximal to its corresponding segment. A certain amount of concentration has taken place at the posterior extremity of the body, in that the sixth, seventh, and eighth abdominal ganglia have migrated anteriorly. The sixth ganglion lies in the posterier half of the fifth abdominal segment, while the seventh and eighth ganglia are situated in the sixth abdominal segment.

Each thoracic ganglion gives off two pairs of nerves. The anterior is slender and supplies the developing wing-buds and all the structures in the anterior part of the segment. It may also send out a short intersegmental nerve. The posterior thoracic nerve is stronger than the anterior and innervates the posterior half of the segment. Soon after leaving the nerve-ganglion it gives off a short nerve to the leg (*lg.n.*, text-fig. 14).

Each abdominal ganglion gives off a single segmental nerve, which, however,

divides into two branches supplying the anterior and posterior halves of the segment. The segmental nerves pass above the oblique sternal muscles, but below the longitudinal sternals. A delicate nerve, given off by the anterior segmental nerve, innervates the median muscle of the eversible gland. From the eighth abdominal ganglion two pairs of nerves pass respectively to the eighth and ninth abdominal segments, indicating that the single ganglion constitutes a fusion of two nerve-centres.

Visceral Nervous System.

The supra-intestinal or stomatogastric nervous system is well developed, but the ventral sympathetic nervous system, while it is probably similar to that of other insects, is very difficult to trace. In connection with the ventral tracheal commissure and the short trachea to the segmental ganglion certain ganglionated nerves were observed, but a median longitudinal nerve could not be distinguished. A pair of long delicate splanchnic nerves arises from the last abdominal ganglion and supplies the hind intestine.

The *stomatogastric nervous system* (Pl. IV. fig. 25) is connected with the pair of cerebral ganglia by means of the *labro-frontal nerves* (*lf.n.*), which meet anteriorly above the pharynx in a triangular *frontal ganglion* (*f.gn.*). A median and a pair of lateral *labral nerves* (*lr.n.*$_2$) are given off from the anterior margin of the frontal ganglion. Posteriorly the frontal ganglion gives rise to a single *recurrent nerve* (*rc.n.*), which passes along the dorsal wall of the pharynx, below the cerebral ganglia. Along its course the recurrent nerve sends out branches irregularly to the walls of the pharynx. The anterior pair of these nerves is relatively long and extends backwards to innervate the intestinal wall near the junction of the œsophagus and crop. Immediately behind the brain the recurrent nerve dilates slightly into a rather inconspicuous *hypocerebral ganglion* (*hb.gn.*), from which a pair of nerves is given off to the small *œsophageal ganglion* (*os.gn.*) lying below the brain. Each œsophageal ganglion effects a connection with the cerebral ganglion of its side by a short anterior nerve. A plexus of nerves (*nl.*) lies antero-laterally to, and appears to originate from, the œsophageal ganglion. Posteriorly the œsophageal ganglion gives rise to a nerve supplying the aorta, and it is also associated with a rather larger *post-œsophageal ganglion* (*op.gn.*) lying at the side of the œsophagus near the posterior margin of the head. From the median hypocerebral ganglion a pair of *stomachic nerves* (*sch.*) passes back along the walls of the crop. They diverge laterally, giving off numerous branches to the walls of the intestine. The main lateral nerve continues to the junction of the fore- and mid-intestines, where a small stomachic ganglion occurs. Numerous short nerves are given off, forming a nerve-plexus in the region of the œsophageal valve.

Sense Organs.

At the extremities of the antennæ and the maxillary and labial palpi there are groups of short broad sensillæ (*tc.p.*, text-fig. 3, A and F), some of which arise directly from the cuticle, while others originate in sockets. They are provided with groups of elongate sense-cells, from which they are innervated. McIndoo (1918–19), who has investigated their structure in certain lepidopterous and coleopterous larvæ, is of the opinion that they are *tactile* and not olfactory in function. They are of general occurrence in Chrysomelid larvæ, but are less well developed in the Galerucinæ than in the other subfamilies. The number of pegs in each group is fairly constant. As a rule six are present on the third antennal joint, while there are usually ten on the maxillary palpus, and from eight to twelve on the labial palpus.

An olfactory sense has been ascribed by McIndoo to certain widely distributed

pores occurring on various parts of the adult and larval integument. In *Paraphædon* and many other Chrysomelid larvæ olfactory pores are of common occurrence on the mouth parts and head-capsule. They are also frequently found on the thoracic legs and around the anal proleg. With very few exceptions a constant number occurs on the trophi of Chrysomelid larvæ, but the number and distribution of the body sensillæ varies in different species.

In *Paraphædon* each joint of the maxillary palpus has one pore, and there is also a pair in front of the three pairs of setæ in the proximal part of the hypopharynx. There are three pores at the base of the median labral incision, and a group of five sensillæ occurs on either side of the epipharynx. The antennæ are also provided with pores, three occurring on the first joint and one on the terminal joint. On each side of the prothorax there is one pore in the anterior half and two in the posterior half of the segment. In the remaining body-segments there is only one sense-organ on each posterior dorsal tubercle.

Each pore is a minute rounded aperture surrounded by a dark peritreme, and resembling a setiferous socket from which the seta has been removed. McIndoo (1918, 19) has investigated their histological structure, and finds that a large sense-cell supplies each pore with a nerve-fibre which passes to the apex of the sensilla and comes into direct contact with the external air. He concludes, from his observations on their histology and from the results of certain experiments, that these sense-organs are olfactory in function, and he has consequently applied to them the term *olfactory pores*.

Ocelli.—The six ocelli on each side of the head are arranged into a dorso-lateral group of four and a ventro-lateral group of two. Each ocellus (Pl. IV. fig. 32) is essentially similar in structure to those of other coleopterous larvæ (Imms, 1925, pp. 71, 75, 77). The cuticle over each ocellus is transparent and constitutes the *cornea* (*c.*), which is thickened to form a biconvex *lens*. Beneath the lens there is a *corneagen layer* of elongate colourless cells which form the *vitreous body* (*vt.*). A dense layer of pigment (*pm.*) lies in the proximal region of the visual cells and forms a kind of iris along the walls of the vitreous body. The cells of the *retinal layer* (*r.l.*), underlying the corneagen layer, are associated with the fibres of the ocellar nerve (*oc.n.*).

Reproductive System.

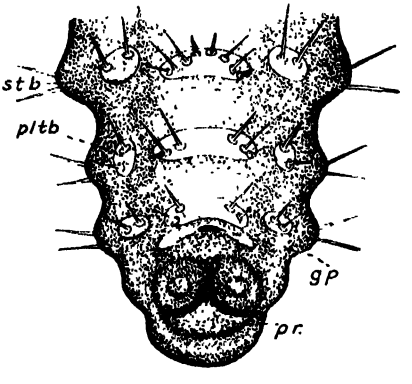
In the larval stage of *Paraphædon* there is little external sexual differentiation, as sexual appendages are not markedly developed. The male larva may be readily recognized, however, by the presence of a minute, dark, transverse slit (*g.p.*, text-fig. 15) on the ventral body-wall, posterior to the ninth abdominal segment. In the female larva there is no such invagination, but occasionally in the mature larva there appear to be indications of the female genital papillæ, which only become evident in the pupal stage. The condition of the efferent ducts and the rudiments of the gonads are markedly different in the two sexes.

In the *male* (Pl. IV. fig. 28) the ventral invagination, which marks the future gonopore, leads into a short wide duct, at the base of which there are several chitinous thickenings, probably the rudiments of the spiculum and lobes of the imaginal genital pocket. The duct is continued as a narrow clear tract, the future *ejaculatory duct* (*ej d.*), lying between a pair of vesicular dilations (*ect.*), into which a filiform *vas deferens* (*vd.*) opens on each side. The lateral swellings are similar in appearance and position to the *ectadenia* of the larva of *Tenebrio molitor* described by Singh Pruthi (1924 *a*), and, as in the latter form, they do not seem to open into the ejaculatory duct. The vasa deferentia, which appear to be solid at this stage, arise about halfway along the lateral margins of the ectadenia. They curve outwards and forwards to the fourth and fifth abdominal segments, in the dorso-lateral fat-body of which the *testes* are situated. Each testis (*ts.*) consists of two rounded lobes connected to the vas deferens by short vasa efferentia.

In the *female* (Pl. IV. fig. 27) the larval reproductive organs and efferent ducts retain their primitive paired condition throughout. The *ovaries* lie in the dorso-lateral fat-body of the fourth and fifth abdominal segments. Each consists of eleven small incipient ovarioles (*ovl.*) projecting mesially from a slender solid oviduct. Each ovariole is provided with a long anterior filament which unites with the filaments of other ovarioles, forming a common anterior *genital filament* (*g.f.*) on each side. The *oviduct* (*od.*) of each side passes directly to the posterior margin of the seventh abdominal segment, where it ends in a slightly dilated ampulla, but does not effect an opening to the exterior. In the sixth abdominal segment there is a small inward projection from the oviduct, the homology of which is not clear.

In view of the fact that the adult generative organs, and especially the efferent ducts, exhibit very little resemblance to those of the larva, it is of interest to attempt to trace the changes which occur during metamorphosis Very little research has been done on the post-embryonic development of the reproductive system in Coleoptera, and there is some diversity of opinion in regard to the homologies of the various structures in the two sexes. Sharp and Muir (1912),

Text-figure 15.



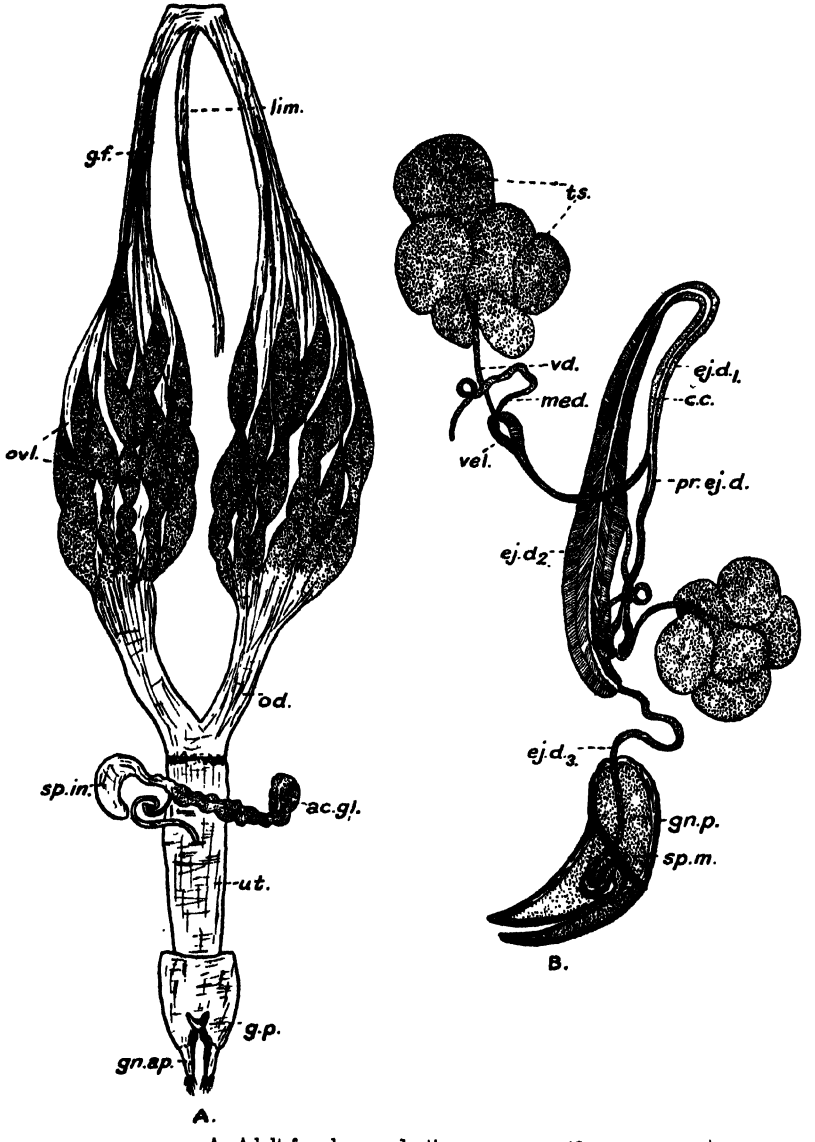
Ventral view of posterior abdominal segments of a male larva. × 46.

Muir (1918), and Singh Pruthi (1924) are almost the only investigators who have undertaken a comparative study of the organs. Muir concludes that the male genital tube arises as a single hollow invagination without any indication of a paired condition, but Singh Pruthi states that "the genital organ in this group (Coleoptera), as in all other groups of insects, does originate as a pair of appendages, and even retains its paired appendage nature till the pupa is three or four days old" (1924, p. 857). The majority of investigators are agreed that the female efferent genital system arises from the ectoderm, but that the position of the genital aperture or apertures varies in different insectan orders.

In the pupal stage of *Paraphædon* the segments are demarcated in both sexes as they are in the larva.

In the *male* pupa and adult the testis lobes (*ts.*, text-fig. 16, B) are more numerous than they are in the larva. They lie in the fourth and fifth abdominal segments in the young pupa, but migrate posteriorly in later pupal life. The vas deferens (*vd.*), which is short and straight, passes back to the seventh abdominal segment, where it joins a somewhat dilated *vesicula seminalis* (*vel.*). The latter probably corresponds with the ectadenia of the larval organs. At the junction of the vas deferens and vesicula seminalis a coiled *mesadenia* (*med.*), which is

Text-figure 16.



A. Adult female reproductive organs. × 43.

B. Adult male reproductive organs. × 43.

developed during the pupal instar, is given off. The genital tube (*pr.ej.d.*) passes forwards and inwards from the vesicula seminalis and unites with that of the opposite side to form a common ejaculatory duct ($ej.d._1$). The ejaculatory duct proceeds to about the second abdominal segment, where it redoubles,

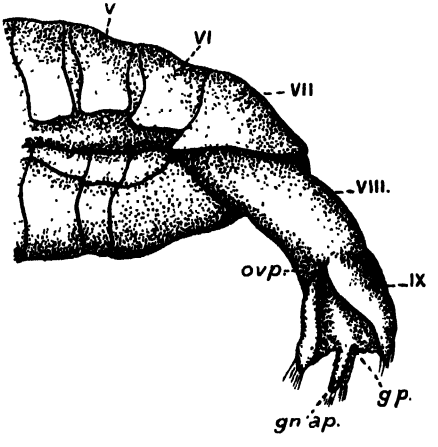
passing backwards as a considerably dilated and muscular tube (*ej.d.*$_2$), lying above and slightly to the right of the hind intestine. It narrows abruptly into a slender tube (*ej.d.*$_3$) which lies in the posterior region of the body-cavity and enters the genital pocket (*gn.p.*) between the lateral lobes. A narrow chitinous canal (*c.c.*) runs throughout the genital duct from the beginning of the vesicula seminalis to the gonopore. The mesadenia and the short vas deferens have no chitinous intima and are mesodermal in origin. In the adult stage the lobes of the genital pocket are strongly chitinized and the arms of the V-shaped spiculum (*spm.*) lie along the outer walls of the pocket and serve as muscle attachments. Harnisch (1915) and other investigators hold the view that the spiculum and other parts of the adult genital armature are derived from the modified eighth and ninth abdominal segments, but Singh Pruthi (1924) has shown that in *Tenebrio molitor* the rudiments of the spiculum are present in the larval stage. A somewhat similar condition obtains in *Paraphædon*, in which the eighth and ninth abdominal segments are retracted within the body at the end of pupal life. They are membranous and lie on either side of the genital pocket, neither of them appearing to have been incorporated into the genitalia. Singh Pruthi is of the opinion that in adult Coleoptera the vasa deferentia do not extend beyond the paired testes, and refers to the two tubes which are present as the "paired ejaculatory ducts." In *Paraphædon*, however, in addition to the paired ejaculatory ducts, a short vas deferens is present anterior to the vesicula seminalis. In the larval stage the gonopore, the genital pocket, and the ejaculatory duct are unpaired. The rudiments of the lobes of the genital armature are very small, and it is probable that they originate as paired invaginations as in *Tenebrio molitor*.

The development of the *female* reproductive organs presents many points of interest. In the larva no evidences of the uterus or spermatheca were observed. In the young female pupa, however, the *spermatheca* (*sp.in.*, Pl. IV. figs. 29 & 30) arises ventrally as a single invagination at the posterior end of the ninth abdominal segment. It extends to about the eighth abdominal segment, on the ventral wall of which another invagination, the *uterus* (*ut.*, Pl. IV. figs. 30 & 31), takes place. Singh Pruthi (1924 *b*) has described the similar occurrence of two invaginations in *Tenebrio molitor*, and has further shown that the two tubes subsequently coalesce to form a single genital duct. Jackson (1880) refers to the two generative openings in larval Lepidoptera, but according to him the anterior is the spermathecal and the posterior the uterine opening. During the pupal stage of *Paraphædon* a secondary fusion of the uterus and spermatheca is also effected. The uterus loses its original external opening on the eighth abdominal segment, but communicates with the exterior at the end of the ninth segment by means of the original spermathecal duct. The spermatheca in an old pupa appears as a narrow tube, arising dorso-laterally from a wide uterus or vagina, which, in consequence of the changes which have taken place, is formed partly from the original uterus and partly from the rudiment of the spermatheca. The *accessory gland* (*ac.gl.*, text-fig 16, A) is formed later as a diverticulum of the spermatheca. In the pupa it is a narrow slightly coiled appendage, but in the imago it dilates considerably. The uterus bifurcates anteriorly into a pair of short wide oviducts (*od.*, text-fig. 16, A), which communicate directly with the ovaries. The ovarioles (*ovl.*) correspond in number with those of the larva, and occupy the greater part of the anterior abdominal cavity. In the imago the genital filaments (*g.f.*) are broad, and unite anteriorly in the middle of the second abdominal segment. A strong median ligament (*lim.*) passes back from the fused filaments, and becomes attached to the wall of the colon near its junction with the ileum.

In the adult female, as in the adult male, there are seven visible abdominal tergites, the first of which is greatly reduced. In both sexes there are only five apparent abdominal sternites, but the first is long and broad and extends as far

back as the third abdominal tergite, in which case it seems to represent a fusion of three sternites. Seven abdominal segments are therefore distinguishable in the adult. In the male the remaining terminal segments do not enter into the formation of the genitalia, but in the female they become incorporated into the long ovipositor (*ovp.*, text-fig. 17) and lie within the abdominal cavity. The eighth segment is almost completely dechitinized and membranous, and its sclerites are indistinguishable. The tergite and sternite of the ninth abdominal segment persist as slightly chitinized dorsal and ventral lobes at the posterior extremity of the ovipositor. The palpiform genital appendages (*gn.ap.*, text-figs. 16, A, & 17),

Text-figure 17.



Lateral view of posterior abdominal segments of adult female, showing everted ovipositor. × 25.

which are situated below the anus, on either side of the genital aperture, arise in the pupa as a pair of fleshy lobes, and cannot therefore represent modifications of abdominal sclerites, as is believed to be the case in some insects.

The preceding ontological observations are of interest, not only in that they afford further evidence regarding the ectodermal origin of the female efferent ducts, but also in that they confirm Singh Pruthi's (1924) investigations, and establish beyond doubt the independent origin in the Coleoptera of the spermatheca and uterus, each of which develops as a single invagination, and not from paired rudiments as in some insects.

Summary of Part I.

No previous account of the biology or morphology of the immature stages of *Paraphœdon tumidulus* Germ. has been published.

The insects are common on *Anthriscus sylvestris* and *Heracleum sphondylium*, but their distribution is somewhat discontinuous.

Yellow elongate-oval eggs are usually laid in débris at the base of the food-plant.

Embryonic development takes two or three weeks, and eclosion is effected by means of short, chitinous, paired, thoracic egg-bursters.

Larval life lasts for 20 to 30 days, during which period there are two ecdyses.

Pupation takes place in the ground and the pupal instar lasts for 10 to 14 days.

There is only one generation in the year.
The pupa is exarate and has a definite chætotaxy.
The larva is eruciform.
Detailed accounts of the internal and external larval anatomy are given.
The larval chætotoxy was studied, and a system of enumeration and nomenclature, applicable to many Chrysomelidæ, has been formulated.

Key to the Lettering of Plates.

ab.lr. Abductor muscle of labrum.
ab.md. Abductor muscle of mandible.
ab.mx. Abductor muscle of maxilla.
ac.gl. Accessory gland in female reproductive organs.
a.cl. Ante-clypeus.
ad.com. Anterior tracheal commissure of head.
ad lr. Adductor muscle of labrum.
ad.md. Adductor of mandible.
ad.mx. Adductor of maxilla.
al.m. Alary muscles.
*am.*1 & 2. Levers of closing apparatus of spiracles.
amp. Ampulla at base of larval oviduct.
an.p. Anterior noto-pedal muscles.
ant.b. Anterior branch of spiracular tracheal trunk.
ant.ex. Anterior extensor muscle of femur.
ap.n. Antennal nerve.
as.pl. Abdominal sterno-pleural muscles.
at. Antenna.
at.a. Antennal tracheal.
at.m. Membrane at base of antenna.
*atn.*1 & 2. Principal cephalic tracheal trunk.
at.p. Conical process of antenna.
atr. Atrium of eversible gland.
a.ts$_1$. Abdominal intersegmental tergo-sternal muscle.
a.ts$_2$. Abdominal anterior tergo-sternal muscles.
b.at. Basantonna.
b.c. Buccal cavity.
b.d. Bulbular termination of chitinous canal of glandular cells.
b.m. Basement-membrane.
b.tr. Trachea supplying the brain.
c. Cornea.
cb.gn. Cerebral ganglion.
c c. Chitinous canal of glandular cells.
cd. Cardo.
ch. Chorion.
cl. Clypeus.
*cl.*1-3. Setæ on clypeus.
cln. Colon.
cl.s. Clypeal suture.
c.m. Circular muscles.
con. Ventral condyle of mandible.
conj. Conjunctive tissue in proximal mesenteron.
c.p. Chitinous abdominal spines in pupæ.
cr. Crop.
c.s. Coronal suture.
c.tn. Corpotentorium.
cu. Cuticle.
cx. Coxa.
dep. Depressor muscle of head.
dep.at. Depressor muscle of antenna.
dg.s. Diagonal sternal muscles.
d.hyp. Depressor muscle of hypopharynx.
dl.g. Dorso-lateral setæ in pupæ.
dl.m. Dorso-lateral longitudinal muscles.
dl.tb. Dorso-lateral tubercles.
dors.tn. Dorsal tracheal trunk.
ds.dil. Dorsal dilator muscles of pharynx.
d.tb. Dorsal tubercles.
ect. Ectoderm.
eg.b. Egg-bursters.
*ej.d.*1-3. Ejaculatory duct.
el. Elevator muscles of head.
em. Epithelium.
ep. Epipharynx.
et. Elytron.
ev.g. Eversible glands.
ev.s. Trachea to eversible glands.
ex. Exuvia.
ex.at. Extensor muscle of antenna.
ex.cx. Extensor muscle of coxa.
*ex.fem.*1-4. Extensor muscles of femur.
ex.gal. Extensor muscles of galea.
ex.mp. Extensor muscles of maxillary palpus.
ext. Extensor muscles.
ex.tar. Extensor muscles of tarsus.
ex.tib. Extensor muscle of tibia.
f. Frons.
f.$_1$-*f.*$_6$. Setæ on frons.
f.b. Fat-body.
f.cs. Fronto-clypeal suture.
fem. Femur.
f.gn. Frontal ganglion.

fl. Flexor muscles.
fl.at. Flexor muscles of antenna.
fl.fem. Flexor muscles of femur.
fl.mx. Flexor muscles of maxilla.
fl.p. Flexor muscle of maxillary palpus.
fl.tar. Flexor muscle of tarsus.
*fl.tib.*1-3. Flexor muscle of tibia.
fl.ung. Flexor muscle of claw.
f.s. Frontal suture.
f.vg. Frontal invagination.
gal. Galea.
g.f. Genital filament.
gl. Gula.
gl.ap. Aperture of eversible gland.
gl.c. Glandular cell.
gn. Gena.
gn.$_1$–*gn.*$_4$. Setæ on gena.
gn.ap. Genital appendage.
g.nc. Guard cell nucleus.
gn.p. Genital pocket.
g.p. Gonopore.
hb.gn. Hypocerebral ganglion.
hd. Head.
hs. Hypostome.
ht. Dorsal vessel.
hy.c. Hypodermal cells.
hyp. Hypopharynx.
hyp.p. Hypopharyngeal sensory pores.
hyp.r. Hypopharyngeal rods.
hyp.sa. Hypopharyngeal setæ.
ilm. Ileum.
int. Intima.
lac. Lacinia.
lb. Labium.
lb.n. Labial nerve.
lb.p. Labial palpus.
lb.tr. Labial trachea.
ld.m. Dorsal longitudinal muscles.
lf.n. Labro-frontal nerve.
lg.n. Nerves to thoracic legs.
lg.tr. Tracheæ to thoracic legs.
lig. Ligula.
lim. Median genital ligament in adult female.
l.m. Longitudinal muscles.
l.pl. Longitudinal pleural muscles.
lr. Labrum.
lr.$_1$, *lr.*$_2$. Labral setæ.
lr.n. Labral nerve.
lr.s. Clypeo-labral suture.
l.s. Longitudinal slits in egg-shell.
ls.m. Longitudinal sternal muscles.
l.tb. Lateral tubercles.
m. Muscles of eversible glands.
md. Mandible.
md.n. Mandibular nerve.
*md.t.*1 & 2. Mandibular tracheæ.
med. Mesadenia.
mes.$_1$, *mes.*$_2$. Proximal and distal divisions of mesenteron.
mg. Mid-dorsal setæ in pupæ.
mn. Mentum.
ms.l. Mesothoracic legs.
ms.s. Mesosternum.
Mt.$_1$, *Mt.*$_2$. First and second series of Malpighian tubes.
mt.l. Metathoracic leg.
Mt.rf. Ramification of Malpighian tubes on wall of colon.
mt.s. Metasternum.
mt.tn. Metatentorium.
m.tu. Tuft of setæ on mesial margin of mandible.
mx.gl. Maxillary gland.
mx.n. Maxillary nerve.
mx.p. Maxillary palpus.
n. Oblique notal muscles in abdominal segments.
n.b. Nucleoli.
n.c. Nucleus.
*n.g.*I.–III. Nerve ganglia in thoracic segments.
N.g. 1-8. Abdominal ganglia of ventral nerve-cord.
nl. Nerve plexus.
n.pl. Noto-pleural muscles.
n.tr. Trachea to nerve ganglion.
ob.m. Oblique muscles.
ob.s. Oblique sternal muscles.
oc. Ocelli.
oc.$_1$–*oc.*$_4$. Ocellar setæ.
oc.n. Ocellar nerve.
od. Oviduct.
oes. Œsophagus.
oes.v. Œsophageal valve.
ol.m. Occlusor muscle of spiracle.
o.n. Optic nerve.
op.gn. Post-œsophageal ganglion.
os.gn. Œsophageal ganglion.
ovl. Ovariole.
ovp. Ovipositor.
pa.ct. Para-œsophageal connective.
p.as. Posterior abdominal tergo-sternal muscles.
p.c. Pericardial cells.
p.cl. Post-clypeus.
pd.com. Posterior tracheal commissure in head.

P.dg. Prothoracic sterno-pleural muscle.
*pd.m.*1 & 2. Pleuro-pedal muscles.
pe. Peritreme of spiracle.
pf. Palpifer.
pg. Palpiger.
pg.b. Chitinous bar at base of labial palpi.
ph. Pharynx.
pl. Prothoracic leg.
pl.tb. Pleural tubercles.
pm. Layer of pigment in retinal cells of ocelli.
pn. Pronotum.
pn.m. Peritoneal membrane.
pn.p. Posterior noto-pedal muscles.
post.b. Posterior branch of spiracular tracheal trunk.
pr. Anal proleg.
pr.ej.d. Paired ejaculatory duct.
p.s. Prosternum.
p.sp. Post-spiracular setæ in pupæ.
pt.com. Post-œsophageal commissure.
pt.m. Peritrophic membrane.
P.ts. Prothoracic tergo-sternal, intersegmental muscle.
rc.n. Recurrent nerve.
rec. Rectum.
reg.c. Regenerating cells in mesenteron.
rev. Reservoir.
r.hyp. Retractor muscle of hypopharynx.
r.l. Cells of retinal layer.
r.lb. Retractor muscle of labium.
r.p. Repugnatorial pores.
*rt.*1–8. Rotator muscles of head.
s. Spiracular opening.
sa. Seta.
sb.gn. Sub-œsophageal ganglion.
sch. Stomachic nerves.
scl. Scolus.
sg.n. Segmental nerve.
sg.tn. Segmental trachea.
sl. Superlinguæ.
sm. Stems of Malpighian tubes.
s.ng. Nerve-ganglion at base of spiracle.
sp. Spiracle.
sp.atr. Spiracular atrium.
spd. Sterno-pedal muscles.
sp.in. Spermathecal invagination.
*s.pl.*1–3. Sterno-pleural muscles.
spm. Spiculum.
sp.r. Spermatheca.
sp.tn. Spiracular tracheal trunk.
st. Stipes.
st.b. Subspiracular tubercle.
str.h. Striated border of mesenteron epithelium.
sum. Submentum.
tar. Tarsus.
tb. Tubercle.
tc.p. Tactile processes.
tib. Tibia.
tm. Torma.
tr. Trochanter.
ts. Testis.
ung. Tarsal claw.
ut. Uterus.
v. Vertex.
v_{1}–v_{11}. Setæ on vertex.
vd. Vas deferens.
v.dil. Ventral dilator muscle of pharynx.
vel. Vesicula seminalis.
ves. Balls of secretion elaborated by mesenteron.
vis. 1&2. Visceral tracheæ.
vl.tn. Ventro-lateral tracheal trunk.
vl.tb. Ventro-lateral tubercle.
v.m. Vitelline membrane.
vt. Vitreous body.
v.tb. Ventral tubercle.
wg. Wing.

Bibliography.

Balbiani, E. G. 1890. Études anatomiques et histologiques sur le tube digestif des *Cryptops*. Arch. Zool. Exper. et Gén. vol. viii. pp. 1 82.

Bauer, A. 1910. Die Muskulatur von *Dytiscus marginalis*. Zeitschr. für Zoologie, Bd. xcv. pp. 594–646.

Berlese, A. 1909. Gli Insetti, vol. i. Milan.

Bertrand, H. 1924. Éclosion de l'œuf chez quelques Chrysomélides. Bull. Soc. Ent. France, pp. 54–57.

Böving, A. G., & Champlain, A. B. 1920. Larvæ of North American Beetles of the Family Cleridæ. Proc. U.S. Nat. Mus. vol. lvii. pp. 575–649, pls. 42–53.

Bruntz, L. 1908. Nouvelles recherches sur l'excrétion et la phagocytose chez les Thysanoures. Arch. Zool. Exp. et Gén. vol. viii. pp. 471–488, pl. xvi.

——— 1909. Sur les néphrocytes des Orthoptères et la dénomination de cellules péricardiales. Arch. Zool. Exp. et Gén. Notes et Revue, vol. ii. pp. xvii–xix.

CANDÈZE, E. 1874. Les moyens d'attaque et de défense chez les insectes. Bull. Acad. Roy. Sci. Belg. vol. xxxviii. p. 805.

CARPENTER, G. H. 1912. The Presence of Maxillulæ in Beetle Larvæ. Trans. of Second Ent. Cong. pp. 208–215.

CARPENTER, G. H., & MACDOWELL, M. C. 1912. The Mouth-parts of some Beetle Larvæ. Q. J. M. S. vol. lvii. pp. 373–396, pls. 35–37.

CHAPMAN, T. A. 1903. A Contribution to the Life-history of *Orina* (*Chrysochloa*) *tristis* Fabr. Trans. Ent. Soc. Lond. pp. 245–261, pls. x. & xi.

CHATTON, E. 1920. Les membranes péritrophiques des *Drosophiles* (Diptères) et des *Daphnies* (Cladocères); leur genèse et leur rôle a l'égard des parasites intestineux. Bull. Soc. Zool. Fr. pp. 265–280.

CLAUS, C. 1862. Ueber die Seitendrüsen der Larve von *Chrysomela populi*. Zeits. wiss. Zool. vol. xi. pp. 309–313.

COMSTOCK, J. H., & KOCHI, C. 1902. The Skeleton of the Head of Insects. Amer. Nat. vol. xxxvi. pp. 13–45.

CRAMPTON, G. C. 1921 *a*. The Sclerites of the Head and the Mouthparts of certain Immature and Adult Insects. Ann. Ent. Am. vol. xiv. pp. 65–103, pls. ii.–vii.

——— 1921 *b*. The Origin and Homologies of the so-called "superlinguæ" or "paraglossæ" (paragnaths) of Insects and related Arthropods. 'Psyche,' vol. xxviii. pp. 84–92, pl. v.

DEVILLE, J. ST. C. 1921. Sur une type de dispersion fréquent chez les Coléoptères. Ann. Soc. Ent. Belg. pp. 390–421.

DONISTHORPE, H. ST. J. K. 1902. The Life-history of *Clythra quadripunctata* L. Trans. Ent. Soc. Lond. pt. i. pp. 11–24, pl. iii.

DUFOUR, L. 1843. Mémoire sur les Vaisseaux Biliares ou le Foie des Insectes. Ann. Sci. Nat. Zool. vol. xix. pp. 145–182.

DU PORTE, E. M. 1920. The Muscular System of *Gryllus assimilis* Fabr. Ann. Ent. Soc. Am. vol. xiii. pp. 16–59, pls. i.–vii.

EMDEN, F. VAN. 1925. Zur Kenntnis der Eizahne der Arthropoden insbesondere der Coleopteren. Zeits. wiss. Zool. vol. cxxvi. pp. 622–654.

EVANS, A. M. 1921. On the Structure and Occurrence of Maxillulæ in the Orders of Insects. Journ. Linn. Soc., Zool. vol. xxxiv. pp. 429–456, pl. 31.

FORBES, W. T. M. 1914. A Structural Study of the Caterpillars.—III. The Somatic Muscles. Ann. Ent. Soc. Am. vol. vii. pp. 109–124, pls. xvii.–xxv.

FRENZEL, J. 1882. Ueber Bau und Thätigkeit des Verdauungskanals der Larve des *Tenebrio molitor*, mit Berucksichtigung anderer Arthropoden. Berliner Ent. Zeitsch. vol. xxvi. pp. 267–316, pl. v.

GAGE, J. H. 1920. The Larvæ of the Coccinellidæ. III. Biol. Mon. vol. vi. no. 4, pp. 1–62, pls. i.–vi.

GARB, G. 1915. The Eversible Glands of a Chrysomelid Larva, *Melasoma lapponica*. Journ. Ent. and Zool. Claremont, vol. vii. pp. 88–97, 2 pls.

GEHUCHTEN, A. VAN. 1890. Recherches histologiques sur l'appareil digestif de la larve de la *Ptychoptera contaminata*. 'La Cellule,' vol. vi. pp. 185–289, pls. i.–vi.

GIRAULT, A. A. 1905. Notes on Short Experiments bearing on the Relation of Larval to Adult Legs. 'Psyche,' vol. xii. pp. 44, 45.

GORKA, A. VAN. 1914. Experimentelle und morphologische Beiträge zur Physiologie der Malpighi'schen Gefasse der Kafer. Zool. Jahr. vol. xxxiv. pp. 233–338, pls. 10 and 11.

HARNISCH, W. 1915. Ueber den mannlichen Begattungsapparat einiger Chrysomeliden. Zeits. wiss. Zool. vol. cxiv. pp. 1–94, 1 pl.

HART, T. H. 1882. Notes on the Life-history of *P. tumidulum* Kirby. 'The Entomologist,' pp. 213, 214.

IMMS, A. D. 1907–8. On the Larval and Pupal Stages of *Anopheles maculipennis*. Pt. I. Journ. Hyg. vol. vii. pp. 291–318, pls. iv., v. Pt. II. Parasitology, vol. i. pp. 103–132, pls. ix., x.

——— 1925. A General Text-book of Entomology. London.

JACKSON, W. H. 1890. Studies in the Morphology of Lepidoptera—Pt. I. Trans. Linn. Soc. vol. v., Zool. pp. 143–187, pls. 15–19.

KEILIN, D. 1917. Recherches sur les Anthomyides à larves carnivores. Parasitology, vol. ix. pp. 325–450, pls. v.–xv.

KEILIN, D. 1921. On the Calcium Carbonate and Calcospherites in the Malpighian Tubes and the Fat-body of Dipterous Larvæ and the Ecdysial Elimination of these Products of Excretion. Quart. Journ. Mic. Sci. vol. lxv. pp. 611-625.

KOWALEVSKY, A. 1889. Ein Beitrag zur Kenntnis der Exkretions-organe. Biol. Centralbl. vol. ix. no. 2, pp. 42–47, 65, 66.

LECAILLON, A. 1898. Sur les Enveloppes ovulaires de quelques Chrysomélides. Arch. Anat. Micr. vol. ii. pp. 89–117, pl. v.

LUBBOCK, J. 1858. On the Arrangement of the Cutaneous Muscles of the Larva of *Pygæra bucephala*. Trans. Linn. Soc. vol. xxii. pt. iii. pp. 173–191, 2 pls.

LYONET. P. 1762. Traité Anatomique de la Chenille qui ronge le Bois du Saule. Amsterdam.

MCINDOO, N. E. 1918. The Olfactory Organs of a Coleopterous Larva. Journ. Morph. vol. xxxi. pp. 113–131.

——— 1919. The Olfactory Sense of Lepidopterous Larvæ. Ann. Ent. Soc. Amer. vol. xii. pp. 65–84.

MARTYNOW, A. 1904. Ueber den Ursprung der peritrophen Hullen bei den Larven der Trichopteren. Zool. Centralbl. vol. xi. pp. 316–318.

MAULIK, S. 1926. The Fauna of British India: Coleoptera, Chrysomelidæ (Chrysomelinæ and Halticinæ). London.

MAYET, V. 1896. Une nouvelle fonction des tubes de Malpighi. Bull. Soc. Ent. Fr. pp. 122–126.

METALNIKOV, S. 1908. Recherches expérimentales sur les Chenilles de *Galleria mellonella*. Arch. Zool. Exp. et Gén. vol. viii. pp. 489–588, pls xvii.-xxi.

MUIR, F. 1918. Notes on the Ontogeny and Morphology of the Male Genital Tube in Coleoptera. Trans. Ent. Soc. Lond. pp. 223 229, pl. x.

NUTTALL, G. H. F., & KEILIN, D. 1921. On the Nephrocytes of *Pediculus humanus*. Parasitology, vol. xiii. pp. 184 192.

PACKARD, A. S. 1898. A Text-book of Entomology. New York.

PAYNE, O. G. M. 1916. On the Life-history and Structure of *Telephorus lituratus* Fallen. (Col.). Journ. Zool. Research, vol. i. pp. 4–32, 4 pls.

POYARKOFF, E. 1910. Recherches histologiques sur la Métamorphose d'un Coléoptère (la Galéruque de l'Orme). Arch. d'Anat. Micr. vol. xii pp. 333–474.

PURI, I. M. 1925. On the Life-history and Structure of the Early Stages of Simuliidæ.—Pt. I. Parasitology, vol. xvii. pp. 295 334, pls. viii., ix.

RIPLEY, L. B. 1923. The External Morphology and Postembryology of Noctuid Larvæ. Ill. Biol. Mon. vol. viii. no. 4, pp. 1 102. pls. i-viii.

SCHINDLER, E. 1878. Beitrage zur Kenntnis der Malpighi'schen Gefasse der Insecten. Zeitschr. wiss. Zool. vol. xxx. pp. 588–660.

SHARP, D. 1910. On the British Species of *Phædon*. Ent. Monthly Mag. Lond. pp. 4-6.

SHARP, D., & MUIR, F. 1912. The Comparative Anatomy of the Male Genital Tube in Coleoptera. Trans. Ent. Soc. Lond. pp. 477 642, pls. xlii.-lxxviii.

SINÉTY, R. DE. 1900. Les Tubes de Malpighi chez les Phasmes (Orthop.). Bull. Soc. Ent. Fr. pp. 333–335.

SINGH PRUTHI, H. 1924 *a*. The Postembryonic Development and Homologies of the Male Genital Organs in *Tenebrio molitor* L. Proc. Zool. Soc. pp. 857–868, pls. i.-iii.

——— 1924 *b*. On the Development of the Ovipositor and Efferent Genital Ducts of *Tenebrio molitor* L. *Ibid.* pp. 869-883, pl. iv.

SIRODOT, S. 1858. Recherches sur les Secretions chez les Insectes. Ann. Sci. Nat. Zool. vols. ix., x. pp. 141–189, 251–334, pls. 9 20.

SMITH, R. C. 1920. The Process of Hatching in *Corydalis cornuta* Linn. Ann. Ent. Soc. Amer. vol. xiii. pp. 70–74.

STEINKE, G. 1919. Die Stigmen der Kaferlarven. Archiv fur Naturg. vol. vii. pp. 1-58, 2 pls.

TOWER, W. L. 1906. Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. Carnegie Inst. Wash. vol. xlviii. 320 pp.

VANEY, C. 1900. Note sur les Tubes de Malpighi des Larves de *Stratiomys* (Dipt.). Bull. Soc. Ent. Fr. pp. 360, 361.

VIGNON, P. 1901. Recherches de Cytologie Générale sur les Epitheliums. Arch. Zool. Exp. et Gén. vol. ix. pp. 371-715, pls. xv.-xxv.

VOINOV, D. N. 1898. Epithelium digestif des nymphes d'*Æschna*. Buletin Soc. de Sciinte, pp. 49–52.

VOINOV, D. N. 1898. Recherches physiologiques sur l'appareil digestif et le tissu adipeux des larves des Odonates. *Ibid.* pp. 472–493, 2 pls.

WADE, J. S. 1921. Notes on the Defensive Scent-glands of certain Coleoptera. 'Psyche,' vol. xxviii. pp. 145–149.

WATSON, M. 1916. Studies on Gregarines. Ill. Biol. Mon. vol. iii. pp. 1–258, 15 pls.

WOODS, W. C. 1916. The Malpighian Vessels of *Haltica bimarginata* Say (Coleoptera). Ann. Ent. Soc. Amer. vol. ix. pp. 391–407.

——— 1917. The Biology of the Alder Flea-Beetle. Maine Exp. Stat. Bull. 265, pp. 250–284.

——— 1918. The Alimentary Canal of the Larvæ of *Altica bimarginata* Say (Coleoptera). Ann. Ent. Soc. Amer. vol. xi. pp. 283–317, pls. xxvi.–xxix.

EXPLANATION OF THE PLATES.

(All the figures on Plates I.–IV., with the exception of fig. 3, refer to *Paraphædon tumidulus*.)

PLATE I.

Fig. 1. Dorsal view of adult. × 11.
Fig. 2. Ventral view of adult, showing keeled prosternum and metasternal line. × 11.
Fig. 3. *Phædon cochleariæ*. Ventral view. × 11.
Fig. 4. *Paraphædon tumidulus*. Embryo seen through egg-membranes. × 40.
Fig. 5. Egg, showing longitudinal slits effected by the chitinous egg-bursters. × 35.
Fig. 6. Tubercle IV. of mesothorax, showing the egg-burster (*eg.b.*). × 580.
Fig. 7. Side view of third-stage larva. × 16.
Fig. 8. Side view of first-stage larva. × 11.
Fig. 9. Side view of pupa. × 14.
Fig. 10. Ventral view of pupa, × 11·5.

PLATE II.

Fig. 11. Longitudinal section of retracted eversible gland. × 213.
Fig. 12. Longitudinal section of single glandular cell. × 520.
Fig. 13. Longitudinal section of wall of œsophagus. × 200.
Fig. 14. Transverse section of wall of œsophagus. × 480.
Fig. 15. Transverse section of wall of crop. × 540.
Fig. 16. Transverse section of wall of proximal region of mesenteron. × 500
Fig. 17. Longitudinal section of first-stage larva. × 100.

PLATE III.

Fig. 18. Transverse section of distal region of mesenteron. × 500.
Fig. 19. Tangential section of wall of alimentary tract at junction of mesenteron and hind intestine. × 140.
Fig. 20. Transverse section of distal portion of ileum. × 500.
Fig. 21. Transverse section of wall of colon. × 487.
Fig. 22. Transverse section of wall of distal portion of colon. × 487.
Fig. 23. Transverse section of wall of rectum. × 340.
Fig. 24. Transverse section of integument and heart, showing pericardial cells. × 490.

PLATE IV.

Fig. 25. Dorsal view of supra-intestinal nervous system. × 100.
Fig. 26. Side view of brain and cephalic nerves. × 100.
Fig. 27. Female larva, generative organs of left side. × 100.
Fig. 28. Male larva, reproductive organs of right side. × 100.
Figs. 29–31. Transverse sections of young female pupa, showing the invaginations of spermatheca and uterus. × 47.
Fig. 32. Longitudinal section of a dorsal ocellus of a young third-stage larva. × 500.

31. On a New Dipterous Parasite (Family Calliphoridæ, Subfamily Calliphorinæ) of the Indian Elephant, with Notes on other Dipterous Parasites of Elephants.

By Major E. E. Austen, D.S.O., F.Z.S.

[Received March 31, 1930: Read April 15, 1930.]

(Text-figures 1–3.)

According to Lieutenant-Colonel G. H. Evans, late Superintendent, Civil Veterinary Department, Burma, the presence of Dipterous larvæ in the subcutaneous tissue of elephants is of very frequent occurrence in that country. In his book, 'Elephants and their Diseases' (Rangoon: Superintendent, Government Printing, Burma, 1910), p. 214, Colonel Evans writes:—"Warbles or swellings due to the invasion of the subcutaneous tissues by the larvæ of one or more of the family Œstridæ (gadflies) are very common in elephants in various parts of the province from the Chindwin to Tenasserim. As a rule they are numerous, but in some cases in the Meza forests mentioned by Mr. Petley, of Messrs. Steel Brothers, the infestation was remarkable. He described it as follows:—

"'The elephants from which these "bots" were taken literally swarm with swellings in all parts—head, ears, and body. The scars of recent eruptions are in some parts of the body so closely pitted as to impart to the skin a honeycomb appearance, showing that thousands of the parasites have burrowed out during the last few months. Curiously enough, only the elephants brought from India last year are affected, and no doubt their general unhealthy appearance is due to the presence of myriads of "bots" beneath the skin. In the elephants from which the specimens were taken the numbers were almost incredible.'

"How the larvæ reach the subcutaneous tissues has not yet been rightly explained. Many theories have been advanced, but the more common one would seem to favour the idea that the egg is deposited directly on the skin, and the larva in the initial stage of its development gains inlet either by the hair follicles or sebaceous glands to its resting place.

"*Symptoms.*—Swellings, so-called boils or warbles, of varying size. When the larvæ are well developed towards the end of April and May (most commonly here) they produce inflammation and suppuration about them, producing the so-called warbles. When the larvæ are ripe they quit their abodes, usually stern first, after widening the openings.

"*Treatment.*—When the nature of the swellings is recognized, a little pressure applied to them will materially assist in setting the larvæ free. The abscesses should be treated in the ordinary manner. The larva of this fly is about ¼ inch long and consists of some nine segments. The larvæ should be destroyed."

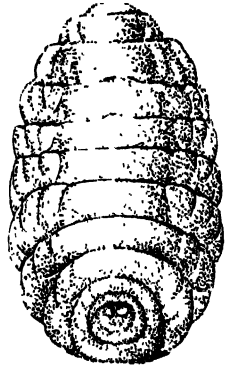
Although Evans furnishes no description of the imago, which he does not appear to have seen, the statement as to the length of the larva would seem to suggest that the species referred to by him is probably identical with the one now described for the first time.

In March 1924 Mr. T. Bainbrigge Fletcher, Imperial Entomologist to the Government of India, applied to the Veterinary Department of Burma for specimens of the larvæ mentioned above, together with any information on the subject that the Department might be able to supply. As the result, several consignments of larvæ were sent in, accompanied by the statement that the specimens had been extracted, apparently during the cold weather, from subcutaneous swellings in

elephants. The material in question was examined by Mr. S. K. Sen, Assistant in the Entomological Section of the Agricultural Research Institute, Pusa, Bihar, India, whose drawing of one of the larvæ is reproduced below (text-fig. 1). According to some unpublished notes by Mr. Sen, kindly supplied by Mr. Bainbrigge Fletcher, the larvæ were of small size (maximum length 5·4 mm.), and, so far as it was possible to judge from preserved specimens, squat appearance, while the greater part of the surface of the body was covered with small, scale-like, flat spines *. Further details noted by Mr. Sen were the incomplete demarcation of the terminal from the penultimate segment, and the character of the posterior stigmatic plates, which were of the Calliphorine type, since each was provided with three straight slits.

Examples of the perfect insect were obtained in the following year, and, on March 27th, 1925, four specimens of the fly described in this paper were received at Pusa from the Veterinary Department of Burma, accompanied by a note in which the sender (Mr. R. M. S. Thursfield) stated :—" On December 30th

Text-figure 1.



Dipterous larva from subcutaneous swelling in Indian Elephant (Burma), × 8.
Drawn (from specimen in preservative fluid) by Mr. S. K. Sen.

. . . I put six live larvæ in a small screwtop jar on the top of some sandy soil, and within five minutes they had all burrowed below the surface to go through the 'pupa' stage. On February 12th I found these four dead flies in the jar. They may have hatched any time after January 19th ; I was not expecting them so soon, and did not examine the jar between these dates. The flies from the other two larvæ may still appear, but possibly these grubs were injured in extraction from the elephant's skin, and have since died."

In June 1925 the four flies mentioned in the preceding paragraph were handed over to the writer by Mr. Bainbrigge Fletcher; but, although the specimens evidently belonged to a genus and species hitherto undescribed, their condition, owing to mould and denudation, was such as to render them unsuitable for description. Subsequently a further series of specimens, conspecific with the foregoing, was received from Mr. Fletcher : these proved to be in a much better state of preservation, and the genus and species are accordingly described below.

* *Cp.* the present writer's figure and description of the larvæ of the Tumbu-fly (*Cordylobia anthropophaga* Grünberg): Journal of the Royal Army Medical Corps, vol. x. fig. 1, pp. 19–21, 1908.

Family CALLIPHORIDÆ.

Subfamily CALLIPHORINÆ VERÆ Villeneuve.

Section *XANTHOCALLIPHORINÆ* Villeneuve (MUSCIDÆ TESTACEÆ Robineau-Desvoidy, *sens. strict.*).

Elephantolœmus *, gen. n.

Allied to Booponus *Aldrich*†, *but distinguishable*, inter alia, *by having a very differently shaped head, including a much longer face and deeper jowls* (*facial angles well below, instead of on a level with, lower margin of eyes*), *as also a quite differently shaped arista, and by latter bearing hairs* (visible under a hand-lens magnifying 15 diameters, nominal, when head is viewed in profile) *on upper side alone* ‡.—*Eyes* wide apart in both sexes (no obvious difference between ♂ and ♀ in this respect, but parafrontals slightly wider above in ♀ than in ♂); *front* (frons) occupying one-third or rather more than one-third of width of head; *jowls* deep, in basioccipital region about equal in depth to half length of eye; a conspicuous, mainly bare, somewhat depressed area running back below eye from each facial angle, narrowing posteriorly, terminating on reaching posterior orbit, and descending anteriorly until it reaches bristles bordering anterior portion of buccal cavity. *Ocellar bristles* relatively well developed, divergent; two pairs of *verticals*, inner pair convergent; *frontal* bristles small, convergent, nine or ten in each row, descending about to level of tip of first antennal segment; ♀ with two, rather inconspicuous, *orbital* bristles (one of them sometimes wanting) on each side, situated high up approximately on a level with interspaces between first and second, and second and third (or third and fourth) frontals. Facial pit long and deep, median carina narrow and low, but sharply defined; vibrissæ small, facial ridges bearing short bristles on lower third or rather less than lower half; facial angles blunt, not prominent but markedly convergent, separated by an interval equal to about one-third of width of facial pit at its widest. *Palpi* clavate; proboscis normal. Third segment of *antenna* large, especially in ♂; basal segments of *arista* very small and short, terminal segment stout—in ♂ tapering to a point rather abruptly at about four-fifths of its length, in ♀ distal third, or rather more, tapering to a fine point; arista feathered above with very short hairs, commencing a little beyond base and not quite reaching tip, some seven or eight of these hairs in middle or towards end of series longer than remainder; in ♂, hairs on arista somewhat shorter than in ♀.

Thorax with a row of from 5 to 7 hypopleural bristles; sternopleurals, 1 anterior, 1 posterior; mesopleurals, 5 or 6; pteropleural, 1; acrostichals, 2 or 3 anterior, 4 or 5 posterior; dorsocentrals, 2 anterior, 4 posterior; humerals 3; posthumerals, either 2 or 3; sublateral, 1; presutural, 1; notopleurals, 2; intra-alars, 3; supra-alars, 3; post-alars, 2 or 3; scutellars, 3 lateral pairs, of which the middle pair is apical, long, and decussating, and three other pairs in a curved line above them, of which the middle pair is discal.

Abdomen without macrochætæ; ventral scutes exposed, posterior margin of fifth visible ventral scute in ♂ deeply cleft.

* Elephantolœmus=a plague to elephants (ἐλέφας, an elephant; λοιμός, a plague or pest).

† *Cf.* Aldrich, J. M., "A New Genus and Species of Fly reared from the Hoof of the Carabao," Philippine Journ. Sci. vol. xxii. pp. 141, 142, 1923.

‡ In *Booponus*, at least as represented by the ♀ of *B. intonsus* Aldrich, which is at present the only described species of the genus, rather less than the proximal half of the terminal segment of the arista is stout, while the remainder of this segment, which, for the greater part of its length, is much less swollen than the corresponding segment in *Elephantolœmus*, is very slender; the arista in *Booponus* is also feathered below as well as above, though the feathering above is much longer than that below.

Wings (*cf.* text-fig. 2): first posterior cell narrowly open just above extreme tip of wing; terminal section of fourth longitudinal vein with a rounded bend, then curved inwards before tip; third longitudinal vein curving towards costa opposite bend of fourth vein, and likewise curved inwards before tip; distal portion of first longitudinal vein, commencing at a point on a level with bent-forward tip of auxiliary vein, sometimes (at least in case of genotype) with one to three small black bristles on upper side, rather wide apart, and not always distinguishable even under a compound microscope; third longitudinal vein with a row of some 5 to 10 black bristles on upper side, from its base to a point about one-half to three-quarters of distance from base of third vein to anterior transverse vein.

Legs: bristles including a single bristle on anterior side of extensor surface of middle tibia, at three-fourths of its length from base.

Genotype: *Elephantolœmus indicus*, sp. n.

Elephantolœmus indicus, sp. n. (Text-figs. 2 & 3.)

♂ ♀.—Length, ♂ (five specimens) 4·8 to 5·5 mm., ♀ (two specimens) 5·8 to 6·0 mm.; width of head, ♂ 2·0 to 2·2 mm., ♀ 2·25 to 2·4 mm.; width of front at vertex, ♂ 0·8 mm., ♀ 1·0 mm.; length of wing, ♂ 4·5 to 5·4 mm., ♀ 5·4 mm.

A compactly built little fly, looking (*apart from the fact that the ♂ is dichoptic*) *not unlike a miniature* Cordylobia*. *Body in ♂ cinnamon-buff*† *or ochraceous-buff, with darker markings on dorsum of main portion of thorax* (*scutum*) *and on distal half of abdomen; body in ♀, except scutellum and lateral and posterior borders of scutum, mainly black or blackish above; frontal stripe in both sexes russet or chocolate; dorsum of scutum in both sexes dull, that of scutellum and abdomen in both sexes moderately shining; wings lightly and uniformly tinged with drab; legs cinnamon-buff.*

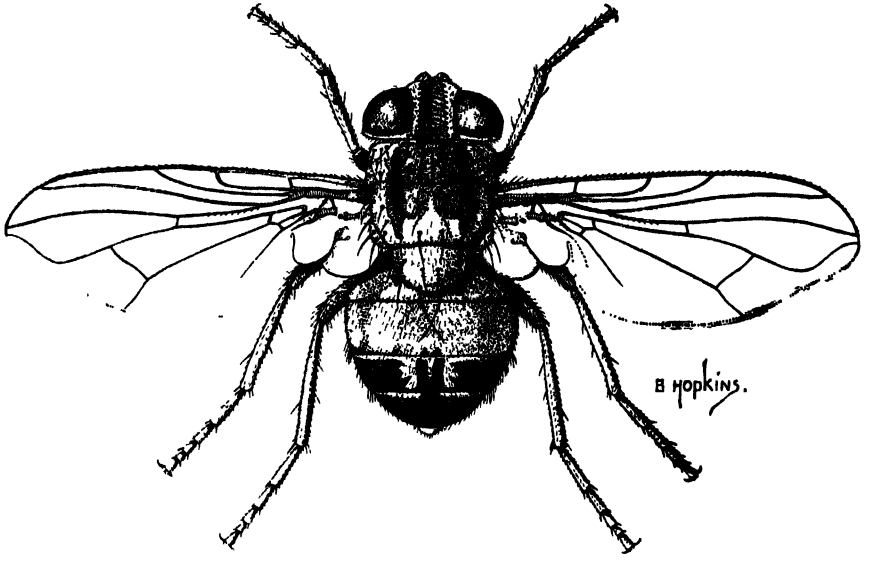
Head: chætotaxy as described for genus, all bristles on head, like those on body and legs, black; parafrontals, parafacials, and ocellar triangle dark olive-grey or iron-grey, clothed like jowls with minute black hairs, parafrontals and parafacials with a pale neutral grey, pollinose covering: a silvery-white, pollinose mark below each eye, occupying lower end of each parafacial (when head is viewed from in front), and a similar, somewhat oblong, pollinose mark below each bare, depressed area; facial pit, except lower border of clypeus, dark mouse-grey; bare, depressed area running back from facial angle above jowl on each side vinaceous-rufous or ferruginous; occiput, jowls, and margin of buccal cavity cinnamon-buff or cinnamon, occiput on each side above with a dark mouse-grey, somewhat triangular mark; posterior orbits pale smoke-grey pollinose; *palpi* ochraceous-tawny, clothed with black hairs; first and second segments of *antennæ* ochraceous-tawny, third segment dark greyish olive or dark mummy-brown, sometimes paler (ochraceous-tawny) on inner side at base; third segment of antennæ longer (3½ to 4 times as long as wide) in ♂ than in ♀ (3 times as long as wide); terminal segment of arista either mummy-brown, or ochraceous-tawny with brownish tip.

Thorax: chætotaxy as described for genus; dorsum including scutellum clothed with minute black hairs, some black hairs on pleuræ also; in both sexes lateral borders of scutum broadly, scutellum entirely, and a more or less quadrate median area in front of latter, not extending further than roughly halfway between base of scutellum and transverse suture, and sometimes considerably less, cinnamon-buff; remainder of dorsum slate-black, with a smoke-grey pollinose covering, showing three narrow longitudinal stripes in median area in front of suture;

* Cf. *Cordylobia anthropophaga* Grünb., the African "Tumbu" fly, the larva of which is a subcutaneous parasite in man, monkeys, dogs, and other animals.

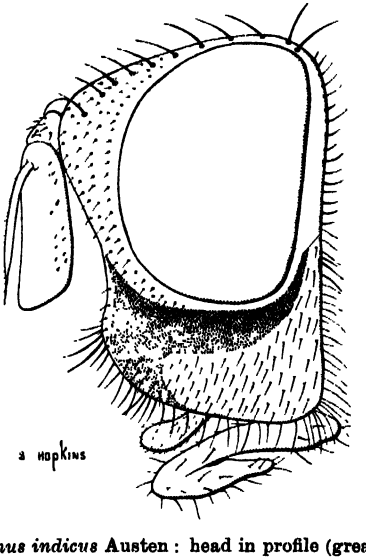
† For names and illustrations of colours used for descriptive purposes in the present paper, see Ridgway, 'Color Standards and Color Nomenclature' (Washington, D.C. Published by the author, 1912).

Text-figure 2.



Elephantolœmus indicus Austen, ♂. × 8¾.

Text-figure 3.



Elephantolœmus indicus Austen: head in profile (greatly enlarged).

pleuræ in both sexes ochraceous-buff, blotched with slate-black or slate colour, meso- and sternopleuræ, except margins, sometimes entirely slate-black, with pollinose covering like that of dark area on dorsum.

Abdomen: clothed above and below with minute black hairs, and with longer hairs on hind margins of segments; third and fourth visible tergites in ♂, except extreme anterior margins, more or less extensively marked with brownish-black, such dark markings consisting essentially of a blotch occupying each lateral extremity of third and fourth tergites (sometimes confined to hind border in case of third tergite), and two admedian longitudinal stripes, commencing near fore border of third tergite and terminating on hind border of fourth; in some cases, in addition to reappearing on hind border of second tergite, these stripes coalesce, while lateral brownish-black blotches on third and fourth tergites are much extended, so that fourth tergite, except extreme anterior margin on each side of coalesced longitudinal stripes, is entirely brownish-black; distal half of venter in ♂, except hind margins of deflexed tergites, which are pale, more or less brownish-black; fifth tergite and external genitalia in ♂ ochraceous-buff; in ♀, first (visible) tergite, lateral extremities of second tergite anteriorly, and extreme hind margins of lateral extremities of same tergite ochraceous-buff or cinnamon-buff, sixth tergite in ♀ sometimes ochraceous-tawny; first (visible) ventral scute in ♀, and second and third ventral scutes in same sex, except hind borders of the two latter, ochraceous-buff or cinnamon buff, ventral scutes in ♀ otherwise black or blackish. *Wings*: veins tawny-olive-coloured, anterior transverse vein and adjacent portion of fourth longitudinal vein, as also distal portion of second longitudinal vein, sometimes more or less mummy-brown. *Squamæ*: alar pair hyaline or nearly so, with thickened border cream-buff; thoracal pair cream-buff, opaque. *Halteres* pinkish-buff. *Legs*: claws black, ochraceous-tawny at base.

Burma: Mawkai.

Type of ♂, type of ♀, and five paratypes (four ♂ ♂, one ♀), bred, 8, 9. ix. 1925, from larvæ which emerged, 30. viii. 1925, from the skin of a dead elephant (Bombay Burma Trading Corporation: types and paratypes in British Museum, presented by Mr. T. Bainbrigge Fletcher).

Writing from the Agricultural Research Institute, Pusa, Bengal, on 6th December, 1926, when forwarding these specimens, Mr. Bainbrigge Fletcher said:—"These were received, through the Burma Veterinary Department, from the Bombay Burma Trading Corporation, Local Agency at Mawkai, Burma, which reported that the 'grubs emerged from the skin of an elephant called *Hpa Moh Loh*, T. No. E. 449, after death'; and that 'the grubs that we obtained from the animal's skin, and that we placed in dry earth on the morning of 30th August [1925], duly hatched out during the night of 8th/9th September. The flies were kept in a muslin-covered jar, and lived for some 48 hours.'" Mr. Fletcher adds:—"It seems fairly evident, therefore, that the larvæ, as previously reported, do burrow in the skin of the elephant."

Strangely enough, the study of the Dipterous parasites of the Indian elephant has hitherto been much neglected, and knowledge of the species of Diptera parasitic in the larval state in *Loxodon africanus* is—thanks in large measure to the recent labours of Messrs. Rodhain and Bequaert—much more extensive than the available information with regard to the corresponding parasites of its Indian representative. It is highly desirable that systematic efforts should be made, both in India and Burma, to obtain living and fully mature "bots" and other Dipterous larvæ from elephants, and to breed out the perfect insects. Were this done, it is possible that more than one new species might still have to be described. As regards *bot-fly* parasites of the Indian elephant, the ordinary stomach-bot is *Cobboldia elephantis* Steel (see below). According to Evans (*op. cit.* p. 268), bots are also found in the pharynx, œsophagus, frontal cavities, and elsewhere. With reference to elephants in Burma, Evans (*loc. cit.*) writes:—"It is by no means uncommon to find *post-mortem* a patch of bots often up to one hundred in number in the gut." He also says:—"That bots find lodgement in the pharynx of the elephant in Burma is

certain. It is not a rare occurrence for an elephant to suddenly commence a sort of coughing or sneezing and blow bots out of the trunk."

The addition of the species described above brings the number of known Dipterous parasites of elephants up to seven, all but two of which, however, occur in Africa and affect the African and not the Indian elephant. The complete list is as follows:—

Family MUSCIDÆ.

Subfamily COBBOLDIINÆ.

Cobboldia elephantis Steel.
Cobboldia loxodontis Brauer.
Rodhainomyia chrysidiformis Rodhain & Bequaert.

Subfamily CUTEREBRINÆ.

Neocuterebra squamosa Grünberg.

Family CALLIPHORIDÆ.

Subfamily CALLIPHORINÆ.

Elephantolœmus indicus Austen.

Family TACHINIDÆ.

Subfamily RUTTENIINÆ.

Ruttenia loxodontis Rodhain.

Subfamily ŒSTRINÆ.

Pharyngobolus africanus Brauer.

COBBOLDIA ELEPHANTIS Steel.

Œstrus elephantis Steel (larva), Medical Examiner, p. 886, 1878.

Cobboldia elephantis Brauer (larva). Wien. ent. Z. vi. Jahrg. p. 218, Taf. iii., 1887; *idem* (imago, ♂ ♀), Denkschr. K. Akad. Wiss. Wien, math.-naturw. Cl. lxiv. Bd. pp. 262–267, figs. 1–18, 1897; Rodhain & Bequaert (imago, third stage larvæ, eggs, pupa), Bull. Biol. de la France et de la Belgique, T. lii. pp. 404–412, 1919*.

The larva of *C. elephantis*, as stated above, is the ordinary stomach-bot of the Indian elephant†. The adult, which, according to Brauer, varies greatly in length, from 12 to 21 mm., is remarkable for its unusual and striking colouration and appearance, having an ochraceous-orange head, deep black body, and purplish-black wings, while the large squamæ, as well as the alulæ and extreme base of the wings

* The bibliography here given is not intended to be exhaustive. For complete bibliographies of this and other species down to the year 1919, see the admirable paper by Rodhain & Bequaert:—"Matériaux pour une Etude Monographique des Diptères Parasites de l'Afrique. Troisième Partie. Diptères de l'Eléphant et du Rhinocéros," Bull. Biol. de la France et de la Belgique, T. lii. pp. 379–465, figs. 1–21, Planche iii., 1919.

† Writing to the author from the Agricultural Research Institute, Pusa, Bengal, on 6th December, 1926, Mr. Bainbrigge Fletcher remarked:—"We have now received some larvæ of *Cobboldia elephantis* from an elephant which died at Mawlaik, Burma, in March 1925. Hitherto we have had no records of *Cobboldia* except from South India."

except the costal border, are snow-white*. The two sexes are well shown in Brauer's coloured figures (1897).

Cobboldia elephantis is represented in the British Museum (Natural History) by a male and female, presented, with their pupa-cases, in 1901 by the late Prof. Friedrich Brauer. With eight other specimens of the same species, these flies were bred out in Vienna, in June 1896, from larvæ obtained in the latter part of May at the Zoological Gardens, Schönbrunn, from two newly-imported Indian elephants, which had left Bangalore some two months earlier. Prior to the breeding-out of these specimens the adult of *C. elephantis* was unknown, and, in his 1897 paper, Brauer refers to the excitement caused in the Entomological Section of the Vienna Museum by the emergence of the first fly, which took place sixteen days after the finding of the larvæ. As is the habit of bots, the latter left their hosts in the early morning, or perhaps during the night. When placed on earth in a glass jar, about 3 cm. in depth and 12 cm. in diameter, covered with damp moss and transferred to a well-ventilated butterfly breeding-cage, the larvæ soon pupated; three days later the puparia were seen to be shining black, hard, and fully mature.

Cobboldia loxodontis Brauer.

Cobboldia elephantis africani seu *loxodontis* Brauer (larva), Denkschr. K. Akad. Wiss. Wien, math. naturw. Cl. lxiv. Bd. p. 267, 1897.

Cobboldia loxodontis Rodhain & Bequaert (larva, ♂ ♀ imago, biology), Bull. Soc. Path. exot. viii. p. 769, 1915; (description of ♂ ♀, third stage larva, and pupa) Bull. Biol. de la France et de la Belgique, T. lii. pp. 412 421, figs. 4-7, 1919; Bequaert (distribution etc.), Bull. Soc. ent. de France, Année 1920, pp. 68 69, 1920.

The larvæ of this species are parasitic in the stomach and intestine of the African elephant (*Loxodon africanus* Blum.). Since *C. loxodontis* is as yet represented in the National Collection only by larvæ, the following brief details with reference to the perfect insect are taken from the lengthy illustrated description by Rodhain and Bequaert (Bull. Biol. de la France et de la Belgique, *loc. cit.*).

♂ ♀. 10–12·5 mm.

♀. *Head* shining reddish-brown, with darker markings; *antennæ* and *palpi* bright red. *Thorax* shining metallic-blue above, dull black on sides and below. *Abdomen* dull black. *Wings* smoky-black, paler at the tip and on the hind border. *Squamæ* smoky black. *Legs* shining black.

♂. *Head*, *thorax*, and *legs* as in ♀, but clothed with longer hair. Dorsum and sides of *abdomen* metallic-blue. *Wings* and *squamæ* smoky-black, former without paler band on hind border.

According to Rodhain and Bequaert (*loc. cit.* p. 413), *C. loxodontis* is remarkable on account of the flattened shape of the adult, more especially as regards the head and thorax in both sexes, and the abdomen in the female, and the insect is consequently somewhat reminiscent of a Hippoboscid.

As regards adult larvæ, the maximum dimensions given by the authors mentioned above are—length 20 to 26 mm., breadth 8 mm.

It is stated by Bequaert (*loc. cit.* p. 69) that *C. loxodontis* is known to occur in the Upper Ivory Coast, Gold Coast, Lake Chad region, Belgian Congo, and Uganda. The larvæ in the British Museum are all from Uganda, and were taken from two

* Such a combination of colours—red or reddish head, black or blue-black body, and black or at least strongly infuscated wings– is rare among Diptera, but, with the exception of the snow-white squamæ, alulæ, and wing-bases, is to be found in certain Ortalidæ (*cf.* the African *Palpomyiella ruficeps* Enderl. and *Bromophila caffra* Macq., and the South American *Dichromyia sanguiniceps* Wied.).

elephants shot by Mr. J. T. Kennedy: one in the West Madi area, Northern Province, in 1928; the other in the West Nile District (Old Lado Enclave), 9.xi.1929.

RODHAINOMYIA CHRYSIDIFORMIS Rodhain and Bequært.

Cobboldia chrysidiformis Rodhain & Bequaert (larva and ♂ ♀ imago), Bull. Soc. Path. exot. viii. p. 773, 1915; (description of ♂ ♀, first- and third-stage larvæ, pupa, mating and oviposition, and egg) Bull. Biol. de la France et de la Belgique, T. lii. pp. 421–432, figs. 8–12, and Pl. iii. fig. 1, A & B.

Rodhainomyia chrysidiformis Bequaert, Bull. Soc. ent. de la France, Année 1920, p. 68, 1920.

Of this species, which is the genotype and sole known representative of the genus *Rodhainomyia* Bequaert (*loc. cit.*), the larvæ, like those of the foregoing, are parasitic in the stomach and intestine of *Loxodon africanus* Blum.

The length of the perfect insect is given by Rodhain and Bequaert as:— ♂, 11 to 12 mm.; ♀, 12 to 13·5 mm. As its trivial name implies, *R. chrysidiformis*, the sexes of which are alike in colouration, at first sight resembles one of the so-called "Cuckoo-wasps" (family Chrysididæ) in shape, as well as in its shining brassy-green or purplish-blue body, and coarsely punctured and finely striated or rugose integument. The anterior portion of the *front* (frons), upper part of the sides of the face, and the *antennæ* are cinnamon-rufous or ochraceous-tawny. The last two (visible) *abdominal* tergites and the hind borders of the upper portions of the four preceding ones are purplish-blue. *Wings* short, nearly hyaline, but with a slight yellowish tinge; veins ochraceous-buff; apex of first posterior cell abruptly closed some distance from wing-margin. *Legs* mainly purplish-black.

According to Rodhain and Bequaert, third-stage (adult) larvæ of *R. chrysidiformis* are always smaller than those of *Cobboldia loxodontis* Br.; the largest larvæ seen by the authors in question were of a dirty white colour, and measured from 14 to 15 mm. in length, by 6 to 7 mm. in greatest width.

The eggs of *R. chrysidiformis* are stated by Rodhain and Bequaert to be deposited, like those of *Cobboldia*, exclusively on the outer sides of the tusks of the host near the lip, in closely-packed regular rows*.

The present species, which is represented in the British Museum by a solitary female from Belgian Congo (Welle district: presented by Dr. E. Roubaud), is said by Rodhain and Bequaert to be only known to occur in Belgian Congo (Welle and Middle Congo regions); the authors referred to add that, at the Werre-Ango and Api (Welle) breeding-stations, the elephants were always infested by this species and *Cobboldia loxodontis* at the same time.

NEOCUTEREBRA SQUAMOSA Grünberg.

Neocuterebra squamosa Grünberg (third-stage larva), Sitzgs.-ber. Ges. Naturf. Freunde zu Berlin, Jahrg. 1906, pp. 46–49, figs. 6–9, 1906; Rodhain & Bequaert (third-stage larva), Bull. Biol. de la France et de la Belgique, T. lii. pp. 381–387, fig. 1, 1919; Rodhain (second-stage larva, pupa, and imago), Ann. de Parasitologie, T. v, pp. 194–198, figs. 1, 2, and Pl. i, fig. 5, 1927.

Neocuterebra squamosa, which is known to occur in Belgian Congo as well as in Cameroon, according to Rodhain and Bequaert (*loc. cit.* p. 384) is probably distributed throughout the forested region of Central Africa. The larvæ of this species have the extraordinary habit of mining in the deep, cartilage-like layer of the plantar surface of elephants' feet. Rodhain (*loc. cit.* pp. 196–198, fig. 2), who

* *Cf.* observations by the late Dr. P. L. Sclater, F.R.S., on egg-masses "somewhat resembling those of the common Blowfly" on the outer side of the tusks of a female Indian elephant: Proc. Zool. Soc. Lond. 1871, p. 145, 1871.

received a male and female of *N. squamosa** from Api, Northern Belgian Congo, together with the puparia from which the specimens emerged, has given a short description of the adult, and the following particulars are taken from this author's account:—

Length of ♀ (larger than the ♂) 22 mm. A large, thick-set fly, dark metallic-blue in colour, with beautiful greenish reflections, especially on the dorsal surface of the abdomen; ♂ and ♀ alike in colouration. *Head* relatively small, front prominent. *Eyes* separated in both sexes, but closer together in ♂ than in ♀. *Antennæ* reddish-yellow. *Thorax* as broad as long. *Abdomen* globular, curved downwards. *Wings* infuscated and long, projecting beyond the tip of the body; first posterior cell narrowly open. *Squamæ* well developed and strongly infuscated. *Legs* black, stout, and of moderate length.

The puparia from which Rodhain's specimens hatched out were respectively 20 mm. long by 11 mm. in greatest breadth, and 16 mm. by 8 mm.; in shape they were elongate oval, with their posterior halves slightly swollen; the posterior stigmata were buried in a deep vertical cleft.

The third-stage larva of *N. squamosa* is described by Grünberg as from 17 to 19·5 mm. long by 11 to 13 mm. broad; oval and biconvex in shape, uniformly covered with circular or toothed, chitinous scales, and with the posterior stigmatic plates lying at the bottom of a depression, and each bearing three separate, long, elliptical clefts.

Like the following species, *Neocuterebra squamosa* Grünb., is at present unrepresented in the National Collection, either by larvæ or adults.

Ruttenia loxodontis Rodhain.

Ruttenia loxodontis Rodhain (third-stage larvæ), Bull. Soc. Path. Exot. T. xvii. pp. 87–92, fig. 1, 1924; *idem* (imago, pupa, and egg), Ann. de Parasitologie, T. v. pp. 198–201, figs. 3–5, and Pl. i. figs. 3, 4, 1927.

The larva of this species, which is a cutaneous parasite of the African elephant, has hitherto only been observed in the elephant-breeding and training establishment at Api, on the R. Werre, in Northern Belgian Congo, where the larvæ from which *R. loxodontis* was described were obtained, and adults were subsequently reared. Larvæ were met with in the hides of four elephants, two adults and two young animals, and, according to Rodhain (Bull. Soc. Path. Exot. *t. cit.* p. 86, 1924), the regions affected were the flanks, shoulders, thighs, and rump; the larvæ have not been noticed in the feet. From the observations of the discoverer (M. Vermeesch), it appears that the presence of these larvæ in the skin produces only a slight reaction. Their occurrence at Api would seem to be seasonal, and to last from the end of September until the beginning of February, which is said to correspond to the dry season in the Welle region. Three adult larvæ first obtained, on being placed on loose earth, immediately burrowed beneath the surface, and the perfect insects made their appearance in about twenty days; unfortunately these specimens subsequently escaped.

The following notes on the different stages are taken from Rodhain's account:—

Imago, ♂ ♀.—Of medium size, 7–8 mm. in length; black with reddish reflections, the two sexes alike in colouration. *Head* small, as broad as the thorax; *eyes* separate in both sexes; *front* not prominent; *antennæ* yellowish-red, third segment brownish, oval, bearing a naked, spatulate arista; palpi globular, proboscis vestigial. *Thorax* and *abdomen* longer than broad, covered with reddish hair, which has a whitish sheen on the last two abdominal segments; abdomen narrowed posteriorly, and slightly curved downwards. *Wings* infuscated and elongate, projecting beyond the body; first posterior cell closed a considerable

* The larvæ from which these were bred were found in litter forming elephants' bedding.

distance before reaching the tip of the wing, and provided with a short appendix, which does not extend to the wing-margin. *Legs* straw-yellow; tarsi tipped with black.

Third-stage larva.—Length 7 to 10 mm., breadth 7 mm.; ovoid, squat, and biconvex, increasing in breadth from the first to the eighth segment; the integument bearing chitinous scales, which anteriorly are sparser and often spiniform; in addition, scales of brown chitin are embedded within the integument; posterior stigmatic plates small, oval, and pale brown in colour, each bearing three straight or very slightly curved, transverse, elongate elliptical openings.

Pupa.—Length (of largest specimens) 9 mm., greatest breadth 6 mm.; pyriform, very slightly flattened from above downwards, and with the broad posterior extremity regularly rounded.

Average duration of pupal stage 24 to 25 days.

PHARYNGOBOLUS AFRICANUS Brauer.

Pharyngobolus africanus Brauer (third-stage larva and puparium), Verh. z.-b. Ges. Wien, xvi. Bd. p. 883, Tab. xix. figs. 1, 1 *a–c*, 1866; Rodhain & Bequaert (third- and second-stage larva and puparium), Bull. Biol. de la France et de la Belgique, T. lii. pp. 388–395, fig. 2, A & B, 1919; Rodhain (imago), Ann. de Parasitologie, T. v. pp. 201–203, fig. 6, and Pl. i. figs. 1, 2, 1927.

Pharyngobolus africanus, the first of the Dipterous parasites of the African elephant to receive a name, and the only member of its genus yet discovered, was described from one of two third-stage larvæ found on August 13th, 1866, in the Vienna Zoological Gardens, in an elephant which died soon after being imported from Africa. The larvæ are attached by their powerful mouth-hooks to the mucous membrane of their host's œsophagus, and it is considered by Rodhain and Bequaert (*loc. cit.* p. 388) that the distribution of the fly is probably co-extensive with that of *Loxodon africanus*, although hitherto the occurrence of the larvæ has seldom been recorded. The authors in question state that they found larvæ of this species in all the elephants that they had the opportunity of examining in the R. Welle region, Belgian Congo. They also obtained specimens from fresh elephant droppings.

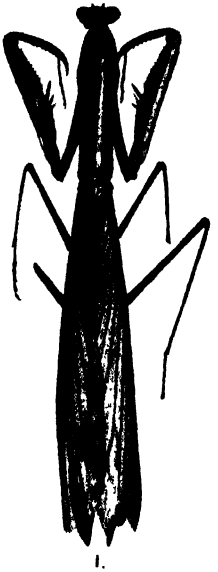
Imago.—Rodhain (*loc. cit.*) describes the adult as a thick-set insect, 15 mm. in length by 6 mm. in breadth, with a large, swollen head, broad and deep thorax, and short straight abdomen. According to the author mentioned, the two sexes exhibit little difference in colour; the ground-colour is black, tinged with greyish, and there are bluish-grey patches on the dorsum of the abdomen. *Head* as wide as deep; *eyes* bare, brick-red in colour, separated in both sexes, but much closer together above, as also much larger in the ♂ than in the ♀, in which they are very wide apart and the front occupies more than half the width of the head; *antennæ* black, sunk in a deep wide pit, arista bare; *proboscis* vestigial; *palpi* absent. *Wings* hyaline, very slightly infuscated towards the base, longer than broad, and with their tips projecting only a very little way beyond the end of the abdomen; distal portion of fourth longitudinal vein angulate and with a short appendix; first posterior cell very narrowly open at the apex, and meeting the costa well before the tip of the wing. *Squamæ* creamy-white, very large. *Legs* black, stout.

Third-stage larva.—Dimensions of four specimens in the British Museum (Natural History):—Length 21–28·5 mm., maximum width 9–10 mm. Colour straw-yellow or brownish-yellow. Third to tenth segments each surrounded with conspicuous circlets of recurved, chitinous, brownish, black-tipped hooks; on the anterior half of each of these segments the circlets are multiple, consisting for the most part of two or three rows of hooks, the rows in the case of mature larvæ being especially distinct on the ventral surface; on the posterior half of each of

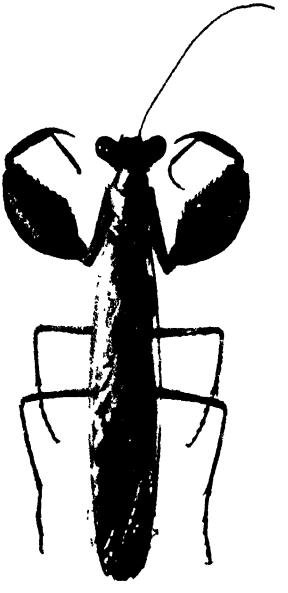
the segments mentioned there is a single ring of hooks, broadly interrupted in the middle of the dorsal surface in the case of the tenth segment; on the eleventh segment, on the dorsal surface the anterior rows of hooks may be reduced to a single row, also sometimes interrupted, while the postmedian row is wanting; on the ventral surface of the eleventh segment the rows of hooklets are as on the preceding segments. Posterior stigmatic plates situated in a deep pit, communicating with the exterior by means of a narrow, transverse cleft.

Pupal stage.—According to Rodhain and Bequaert (*loc. cit.* p. 394), the adult larvæ let go their hold of the wall of their host's œsophagus, and are carried along through the stomach and intestine until expelled *per anum*; they may be found in the morning in fresh elephant droppings, but, since they bury themselves in the soil before pupating, no pupæ are to be met with in old deposits. The authors in question state that pupæ obtained by them from larvæ voided naturally measured about 15 mm. in length by 8 mm. in breadth at their widest point. Seen from above, they were nearly regularly oval in shape, with the anterior margin bluntly rounded and the posterior extremity slightly broader. In profile the dorsal surface of the pupa is strongly convex, the ventral slightly so or almost flat. The colour of the puparium is black and the surface is slightly polished. The duration of the pupal stage is given by Rodhain and Bequaert as from twenty to twenty-one days.

Pharyngobolus africanus is represented in the National Collection by four third-stage larvæ from Uganda (Bunyoro, Masindi), 23. viii. 1929, found, with numbers of similar specimens, by Mr. H. V. C. Sutherland in the pharynx of an elephant, chiefly at the junction of the thick part of the trunk with the head (presented by Captain C. R. S. Pitman, D.S.O., M.C., Game Warden, Uganda Protectorate).

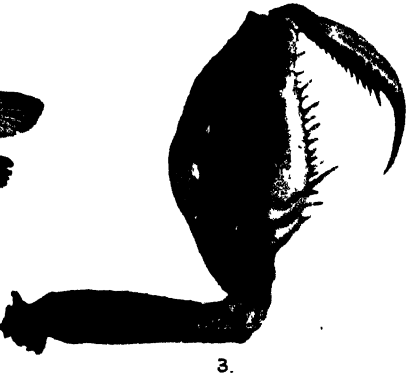


1.





2.



3.

John Bale Sons & Danielsson, Ltd London

INDIAN MANTIDS.

32. Indian Mantids or Praying Insects.

By F. Werner, C.M.Z.S. (Vienna, Austria).

[Received March 10, 1930: Read April 15, 1930.]

(Plate I.*)

By the courtesy of the authorities of the Forest Research Institute, Dehra Dun, India, I had the opportunity to examine a small, but very interesting collection of Mantids from Dehra Dun and some other Indian localities. It contains eight species, among which three proved to be new to science, as well as some others which are rare in collections. They are listed as follows :—

Eomantis guttatipennis (Stål).

♂ from Gauhati, Assam, M. Bose, 29. v. 1927.

Mediastinal and anterior radial vien distinctly separated and transverse veinlets in the space.

Caliridinæ.

Leptomantis indica Giglio-Tos.

♂ from Gauhati, Assam, M. Bose, 29. v. 1927.

No lateral black line of pronotum, as occasionally in other species of the genus. The difference from *L. lactea* (Sauss) is rather trifling, and the species may have to be united to the Malayan one.

Mantinæ.

Mantis nobilis Brunner, 1892.

This rare species seems not to have been found previously but in Burma. Three fine ♂ ♂ from Dehra Dun (23 ix. 1920; 3. viii. 1923, M. Bose; 23. vii. 1927) agree perfectly with Brunner's description.

Mantis inornata, sp. n. (Pl. I. fig. 1.)

1 ♀ from Dehra Dun.

Very closely related to *M. religiosa* L., but distinguished at once by lacking the black elliptical spot at the inner side of anterior coxæ. Costal area brown to the costal vein, which is yellowish; a similar brown band along the mediastinal vein; most of the transverse veinlets likewise brown.

Total length 75 mm.; pronotum 25, elytræ 52 mm. We know hitherto no other species of *Mantis* devoid of any marking at anterior femora or coxæ; this character alone warrants sufficiently the distinctness of the new form.

Vatinæ.

Æthalochroa ashmoliana (Westwood 1841).

2 ♀ ♀, one from Dehra Dun, 29. x. 1924, the other from Etawah, U.P., 27. viii. 1928.

* For explanation of the Plate, see p. 690.

HYMENOPODINÆ.

HESTIASULA BRUNNERIANA Sauss, 1871.

This handsome Mantid is represented in the collection by three specimens, all males, from :—

Dehra Dun, Students coll., 20. viii. 1923 and x. 1928. Nilambur, Madras, S. N. Chatterjee, 4. ix. 1925. All are quite typical.

HESTIASULA NIGROFEMORATA, sp. n. (Pl. I. figs. 2 & 3.)

♂ (type) and ♀ (paratype) from Dehra Dun, Students coll., ix. 24.

♂. Anterior femora, tibiæ and tarsi dark brown, coxæ yellowish brown ; inner side of anterior femora black, perfectly smooth, with a small, whitish round spot in the basal third, near the lower border. Body dark brown, three anterior segments of abdomen blackish, shining smooth, anterior wings greyish brown, hyaline, feebly infumate, transverse veinlets brown; posterior wings perfectly hyaline, only anterior (costal) margin and tip dark brown. Vertex without any tubercle ; organs of flight reaching beyond tip of abdomen. Borders of pronotum entire.

♀. Stouter, anterior wings dark brown, opaque, anterior margin beyond mediastinal vein yellowish brown. Vertex with triangular protuberance ; organs of flight reaching beyond abdomen; otherwise like the male. Borders of pronotum denticulated.

Dimensions :—

Total length, ♂ 19·5; ♀ 22·5 mm. Anterior wings, ♂ 17, ♀ 20·5 mm.; pronotum, ♂ 2·5, ♀ 3·5 ; anterior femora, 5 mm. long, 2·5 broad in ♂, 7·5 long, and 3·5 broad in ♀.

EPHESTIASULA INTERMEDIA, sp. n. (Pl. I. fig. 4.)

♂ (type). Dehra Dun, Students coll., 15. vii. 1927.

Paratypes (♂) from the same locality, 2. viii. 1925, x. 1928, and (F. Z. Coll.), 25. x. 1910.

Perfectly intermediate between *E. amœna* (Bol.) and *E. pictipes* (W. Mason), having the dark median pronotal stripe of the former and the coloration of the inner side of anterior femora quite as the latter, but without any tubercle of the vertex. Anterior wings, costal area greenish, opaque, with irregular veins; pronotum yellowish, dark median longitudinal stripe black ; anterior limbs orange on the inner side, femora with black superior margin and with elongate black spot, containing two white ones, on the inferior margin ; anterior tarsi black ; intermediate and hind limbs yellowish brown. Posterior triangular processes of head short, blunt

Total length 17 mm., pronotum 2·5 (2 mm. broad), anterior wings 17, anterior femora 5 (2·5 broad).

As this species lacks entirely a tubercle of the vertex, it cannot be regarded as connecting the other species ; it is nearer to *pictipes* than to *amœna*.

The genus *Ephestiasula* Giglio-Tos, if it can be altogether maintained—I personally do not admit the necessity of separating it from *Hestiasula*,—is restricted to the mainland of India. The locality of *E. amœna* is, by the way, apparently misspelt by Giglio-Tos as " Rodaikanal," as it is really. " Kodaikanal."

EXPLANATION OF THE PLATE.

Fig. 1. *Mantis inornata*, sp. n.
2 & 3. *Hestiasula nigrofemorata*, sp. n.
4. *Ephestiasula intermedia*, sp. n.



OVARY OF *Papio hamadryas.*



UTERUS OF *Macaca radiata.*

33. The Menstrual Cycle of the Primates.—Part I. General Nature and Homology.

By S. ZUCKERMAN, M.A., M.R.C.S., L.R.C.P., Anatomist to the Society, and Demonstrator of Anatomy, University College, London.

[Received February 4, 1930: Read May 6, 1930.]

(Plates I. & II.; Charts 1–14; Diagrams 1–4.)

CONTENTS.

	Page
I. Introduction	691
II. Breeding Season	693
III. Prominent Features of the Cycle	696
OLD WORLD MONKEYS	697
Family PONGIDÆ	697
Genera:	
1. *Gorilla*	697
2. *Pan*	697
3. *Pongo*	698
Family HYLOBATIDÆ	698
Family CERCOPITHECIDÆ	699
Genera:	
1. *Pithecus*	699
2. *Cercopithecus* and *Erythrocebus*	699
3. *Cercocebus*	700
4. *Macaca*	701
5. *Cynopithecus*	708
6. *Theropithecus*	708
7. *Papio* and *Mandrillus*	708
NEW WORLD MONKEYS	716
IV. Physiology of the Sexual Skin	717
V. Nature and Changes of the Sexual Skin	723
VI. The Biological Significance of the Sexual Skin	725
VII. Puberty	731
VIII. Pregnancy and Lactation	732
IX. Changes in the Ovary and Accessory Organs	737
X. Discussion	742
Summary	748
Bibliography	750
Explanation of the Charts	754
Explanation of the Plates	754

I. INTRODUCTION.

Enough is known of the œstrous cycle of mammals with restricted breeding seasons to enable one to make certain safe generalisations. Seasonal sexual behaviour is related to seasonal physiological activity of the reproductive tract. During anœstrus the generative organs are relatively inactive and shrunken in size. During a breeding season they undergo a definite cycle of changes, and

these cyclical physiological changes are reflected in the cycle of behaviour patterns exhibited by the animal. The maturation of ovarian follicles is associated with the secretion of the follicular hormone, "œstrin," and coincides with a growth-phase in the mucous membrane of the uterus and the vagina. This phase is the proœstrus, the period when the animal is coming into heat. Ovulation is in most animals spontaneous and, with the consequent cessation of activity of the follicular hormone, the hypertrophied mucous membrane of the uterus and vagina degenerates. This is the period of œstrus, which, almost without exception (but see footnote, p. 730), is the only time when the female lower mammal will mate. After ovulation, corpora lutea develop in the ruptured follicles, and the hormonic activity of these organs is responsible for a further growth-phase in the uterine mucous membrane. This luteal phase is concerned with the maternal functions and responses of the animal. Its fullest expression occurs when pregnancy has resulted from mating during the preceding œstrus. If pregnancy has not occurred, the phase is known as pseudo-pregnancy, and this varies in different animals, both in duration and in its effects upon behaviour. Pseudo-pregnancy terminates with destruction of the hypertrophied endometrium, and after this there occurs a short period of regeneration. In monœstrous mammals this regeneration is succeeded by the anœstrus, and in polyœstrous mammals, after a resting phase varying in duration in different animals, by another proœstrus which ushers in the next œstrous cycle, anœstrus finally terminating a succession of œstrous cycles.

These facts have been established by numerous researches on many varieties of lower mammals, and it is very probable that the general principles revealed by these experimental studies are applicable to all mammals, including the primates. Unfortunately, however, less is known of the breeding habits of monkeys and apes than of almost any other group of mammals, and such facts as are known do not obviously fall into any general plan.

Systematists recognize some three hundred species of Old World primates, included in about twenty genera, and about one hundred and fifty species of New World monkeys in twelve different genera. Almost nothing is known of the reproductive physiology of the New World group. Naturalists' accounts of their breeding habits are both rare and meagre, while the only experimental study which has been published is that of Lucas, Hume, and Smith (1927) on the effects of ultra-violet light upon the fecundity of captive marmosets, *Hapale jacchus*. More attention has been paid to the Old World group of primates. A few superficial accounts of the more obvious facts of their reproductive mechanisms exist, while more extensive researches have been made on three species, the rhesus macaque, *Macaca mulatta*, the common macaque or crab-eating macaque, *Macaca irus*. and the entellus langur, *Pithecus entellus*. These latter studies (Heape 1894 etc., Van Herwerden 1906, Corner 1923 etc., Allen 1926 etc., Hartman 1927 etc.) have mainly aimed at correlating the uterine with the ovarian cycle.

Clearly such limited knowledge does not justify any broad generalisation. Nevertheless it is usually stated, as though it were an established fact, that primates differ from lower mammals in that they do not experience either anœstrus or œstrus. Marshall, for instance, writes (1927) that "it is clear that there is ordinarily no anœstrum in the Primates," and Miller (1928) states that "all monkeys differ conspicuously from other mammals in the absence of periodic 'heat.'" Marshall's generalisation, however, is by no means proved, while Miller's statement is certainly incorrect. Baboons, for instance, manifest a well-marked follicular phase, and a distinct period of "heat."

The possible occurrence of anœstrus and œstrus in the reproductive life of the primate is obviously a consideration of the greatest importance in any attempt to

homologise the menstrual cycle of primates with the œstrous cycle of lower mammals.

The human female does not manifest any obvious signs of a follicular phase in her menstrual cycle. Moreover, available data about the human cycle have been gleaned mainly from the operating and post-mortem tables. But though such data are necessarily limited, certain facts are well established. It is known (Shaw 1925) that the catamenia is followed by a short period of regeneration, then by a resting period, and finally by a growth-phase in the endometrium, commencing about the middle of the cycle and terminating at the succeeding catamenia. It is essential to know the time of ovulation in the menstrual cycle in order to interpret the phases of the human endometrium in terms of the phases of the œstrous cycle of the lower mammal. From the evidence of laparotomies, it is believed that in woman ovulation occurs about the middle of the cycle. This generalisation, however, is not fully established and rests upon comparatively few observations. In the lower mammal ovulation, which occurs at the end of the follicular phase of the œstrous cycle, may be readily recognized apart from direct laparotomy. Ovulation coincides with œstrus, which is indicated by œstrous behaviour. Moreover, in many mammals the ovarian cycle may be followed by means of the coincident vaginal changes. In women, however, there is no readily recognizable period of œstrus, and it is still uncertain whether women undergo a vaginal cycle. The vaginal smear technique has thus far yielded different results in the hands of different workers.

On the other hand, in many monkeys the determination of the time of ovulation is comparatively straightforward. The vaginal smear technique applied by several workers to *Macaca mulatta* (= *Macacus rhesus*) shows that this animal experiences cyclical vaginal changes, which in turn have been correlated with the ovarian cycle. It is probable that other primate species also undergo a vaginal cycle. Also, as will be shown later, in many sub-human primates the maturation and rupture of the ovarian follicle bears a definite relationship to cyclical coloration and swelling of the skin around the female external genital organs. These external changes afford a valuable indirect means of inferring the ovarian phases.

The object of this paper is to explain the homology between the œstrous and menstrual cycles. This will be done, not by focussing attention upon any one particular primate species, but by bringing together facts about the cycles of as many primate species as have been observed. In addition to a review of the literature, new data will be presented, obtained from observation of living animals in the collection of the Zoological Society of London and from post-mortem examinations. This paper will serve as an introduction to a series of further studies on the menstrual cycle, already begun by Dr. A. S. Parkes, of University College, London, and myself.

The names of primate species in this paper are those appearing in the revised Vertebrate List of the Zoological Society of London (1929), prepared by Major S. S. Flower.

II. The Breeding Season.

The evidence adduced in support of the view that primates do not experience an anœstrus is derived mainly from two sources; from the observed behaviour of monkeys and apes in captivity and from the reports of field-workers. It is doubtful, however, whether one may infer the reproductive habits of monkeys in a state of nature from observation of the same monkeys in captivity. The distinction between "wild animals in a state of nature, wild animals in captivity, and domestic animals," pointed out by Heape in 1900, is an important one.

Artificial conditions have the effect of increasing reproductive activity by prolonging the breeding season or by increasing the number of such seasons.

Parkes and Brambell (1928) investigated the underlying causes for the anœstrous cessation of reproductive activity in Rodents, and arrived at the conclusion that it could be "attributed to a diminished food supply under conditions of temperature which, for the maintenance of normal function, would require an increase in food."

It would seem, therefore, that the use of data derived from captive animals in the solution of the problem of the occurrence of anœstrus amongst primates is highly questionable. While it is true that most primates breed at any time of the year in captivity, if they breed at all, it is possible that captivity has already deranged their normal reproductive functions.

Heape (1894) was informed that *Macaca mulatta* (=*Macacus rhesus*) bred freely in the Calcutta Zoological Gardens all the year round, and according to Corner (1923 *b*) the same occurs in the National Zoological Gardens in Washington.

In Hartman's experimental colony of rhesus macaques, kept in the United States, "the optimum time for conception," as judged by nineteen pregnancies, is from October to January. The summer months, May to August, Hartman considers to be the non-breeding season. Twelve laparotomies performed on different females in June and July showed inactive ovaries. Hartman infers, therefore, that ovulation does not occur during these months, "although menstruation often, though not always, goes on with perfect regularity" (1929*f*).

Births amongst primates have not been common in the London Zoological Gardens, seventy-five only being recorded in the past hundred years. *Macaca mulatta* and *Macaca irus* were responsible for about half of this number, and both these and the others were scattered sporadically through the year. About fifteen births have occurred in a colony of Hamadryas baboons, *Papio hamadryas*, introduced in 1925. With one exception these have occurred in the last four months of the year. This is certainly suggestive of a breeding season.

It is difficult to know how one is to arrive at the truth about primates and anœstrus from the accounts of travellers. Many of them describe breeding seasons, but their criteria vary. Some talk of rutting seasons, others of pairing seasons, while some again state that young are born only at one time of the year. Moreover, opinions about the same species sometimes conflict with each other. It is, of course, possible that the same species produces young at different times of the year in different localities; but it is hardly likely that, as has been reported, one species in some places gives birth in a particular season, while in other places it does so throughout the year.

Marshall (1927) states that "ordinarily" no anœstrum occurs in Primates, and in his 'Physiology of Reproduction' (1922) he writes that "whereas monkeys may have a continuous series of dioestrous cycles usually at regular monthly intervals, they are not necessarily capable of breeding at every heat period." He draws his evidence for these statements from Heape (1894, 1896), Reade (1864), Burton (1876), Hingston (1920), and Van Herwerden (1906).

I shall examine these statements below as well as certain others collected from the literature.

Winwood Reade (1864), who obtained all his information from native hunters, states that the male gorilla experiences a rutting season. According to Yerkes (1929) this was also Famelart's opinion. Burton (1876), whose information also came from natives, states that the gorilla breeds about December, while Dyce Sharpe (1927) writes from personal observation that gorilla young are seen most commonly about February and March, the season after the early rains. Yerkes (1929) quotes a report of Wilbert's, of the African Station of the Pasteur Institute, that the Chimpanzee "mates during the rainy season, August to October, and gives birth to young more especially from June to September. Sexual intercourse may occur throughout the year, and births are not strictly limited to any one season."

Westermarck (1921) quotes Mohnike in support of the view that the orang-utan experiences a sexual season, and states that Wallace told him (Westermarck) that he "found the young sucking orang-utan in May; that was about the second or third month of the dry season, in which fruits began to be plentiful." Huxley (1863) writes, on the authority of Müller and Schlegel (1839–45), that the old male orang, "except in the pairing time," lives alone. On the other hand, Hitzheimer and Heck (quoted by Briffault 1927) hold an entirely different view about the apes (and monkeys), maintaining that they breed throughout the year.

According to Tickell (1864), whose knowledge of the fauna of the Malay Peninsula was very extensive, the young of gibbons "are born generally in the early part of the cold weather. . . . The young one sticks to its mother's body for about seven months." Tickell does not indicate whether or not this statement is based on personal observation.

It is worth while quoting Heape's statements (1900, 1894) regarding *Pithecus entellus*, the Entellus langur, in full. In 1900 he wrote, referring to his 1894 work, "*Semnopithecus entellus*, from the jungles on the south bank of the Hugli, has a definite time for reproduction." In 1894, however, he was far less definite. He had obtained one hundred and eight specimens of *Pithecus entellus* from collectors. Of these "a considerable number had already borne young, and were suckling them; six were found to have very lately borne young, and one to be undergoing the process of aborting an advanced embryo; the rest were not breeding, and about fifty of these, adult females, were killed. . . .

"I was informed by the dealer—a Eurasian—who supplied me with these animals, that *S. entellus* breeds twice a year, in April and October, and that, when breeding, they retire into the thickest parts of the jungle, and cannot then be caught. This information was doubtless obtained from native collectors, and all evidence supplied by natives was found to be so untrustworthy that little reliance can be placed upon this report

"Bearing in mind the fact that the animals examined were either not breeding, or else had recently borne young, it would seem fair to assume there are one or more limited breeding seasons for *S. entellus*, but my information warrants no further assumption."

There is a great difference between this statement and that of 1900, which is the one more frequently quoted.

Blanford (1888) remarks that the Himalayan langur has a breeding season, but does not state whether or not this opinion is based on his own observation.

Little is known of the genus *Cercopithecus*. The only information I can find is a statement by Fitzsimons (1919) that the Vervet monkey of South Africa, *Cercopithecus pygerythrus*, breeds in December and January.

There are several statements regarding the genus *Macaca*, of which that of Heape's (1894 and 1896) is by far the most important. Not less than four-fifths of several hundreds of *Macaca mulatta* (=*Macacus rhesus*) sent him alive in February and March "bore advanced embryos *in utero*, or had lately borne young, or had recently aborted the embryo." Heape came to the very reasonable conclusion that this was "strong evidence in favour of the assumption that *M. rhesus* has one or more definite breeding seasons." Because of a statement of Mr. Sányál that this species bred at any time of the year in the Calcutta Gardens, Heape was led to believe that the species bred "at different times in different parts of the continent."

According to Hingston (1920) the Himalayan rhesus mates only once in a year, in September, the young being born in March. This opinion is apparently based on personal observation.

Opinions differ about *Macaca irus* (=*Macacus cynomolgos*), the common macaque. Ridley (1895) writes, from personal observation in the Malay States, that this species breeds even in confinement at only one period of the year. This,

too, is the opinion of Van Herwenden (1906), who writes that this species (incorrectly named *Cercocebus*) breeds in the Island of Banka, as a rule, only in August, September, and October. On the other hand, Blanford (1888), whose experience of the mammalian fauna of India and the Malay States was second to none, writes that in this species "there is no particular season for breeding."

The Gibraltar ape, *Macaca sylvana*, has been closely observed, living as it does in a state of semi-domestication. According to Sclater (1900) and C. H. (1880), the young of this species are born in spring and early summer.

Little is known of the genus *Papio*. Stevenson-Hamilton (1912) writes, from personal observation, that the young of *Papio porcarius*, the Chacma baboon, are born between November and February. (I myself once shot in January a female of this species carrying a newly-born infant.) Loveridge (1923), however, writes that the yellow baboon of East Africa, *Papio cynocephalus*, breeds throughout the year. As basis for his opinion, he states that he has seen females with young in May, July, August, and October, though he gives no details about the size of the young.

I know of only a few records of the breeding of South American monkeys. Rengger (1830) states that *Alouatta caraya* breeds usually in June or July, sometimes towards the end of May, and sometimes in August; *Cebus azaræ* in December; and *Aotes trivirgatus* between June and September. The same author, according to Forbes (1894), states that the young of the Weeper capuchin (*Cebus apella*) are born in January.

Hofschläger (1925), after stating that man and monkeys differ from other mammals in having no particular breeding season, remarks that this does not apply to all primates, for, according to Rudolf Hermann, who has corroborated the statements of Spix and Martius, monkeys in the neighbourhood of the River Amazon breed in the last months of the year.

From the work of Lucas, Hume, and Smith (1927), it is known that in captivity the common marmoset, *Hapale jacchus*, produces young twice a year. Miss Hume tells me that there is a tendency for births to group towards spring and autumn even when a comparatively long interval elapses between the pregnancies of any particular female.

The greater number of these reports of naturalists indicate breeding seasons. Apart from the accounts of *Macaca mulatta* and *Macaca sylvana*, however, one would require confirmatory evidence before accepting them. Moreover, as with our present knowledge it is impossible to state with certainty whether non-pregnant mature females do or do not menstruate throughout the year, it is impossible to judge whether or not anœstrus is experienced by any primate.

III. Prominent Features of the Cycle.

References are occasionally encountered in the literature to cyclical variations in the conformation and coloration of the perineal region of infra-human primates. In Cuvier's 'Animal Kingdom' (1834, p. 52), for instance, attention is drawn to such changes in the genus *Macaca*. "During the rutting season the labia pudendi, &c., of the females are excessively distended. . . . Hence the observation of Aelian that monkeys are to be seen in India which have a prolapsus uteri" *. The same genus was singled out for note by Darwin (1871) in his argument on sexual selection. The female rhesus macaque "has a large surface of naked skin round the tail, of a brilliant carmine red, which, as I was assured by the keepers in the Zoological Gardens, periodically becomes even yet more vivid, and her face also is pale red." In 1876 Darwin, in a contribution to 'Nature,' laid further emphasis on this phenomenon in *Macaca mulatta* (=*Macacus rhesus*) as a factor in

* Many of the early pictures of anthropoids (see Yerkes, 1929) show the animals with a caudal swelling.

sexual selection, comparing it with the bright coloration of the male mandrill. Breschet (1845) quoted some notes given him by his colleague, M. Isidore Geoffroy-Saint-Hilaire, on the subject of the menstrual cycle of monkeys. "Les femelles des *Guenons*, des *Macaques*, des *Magots*, des *Cynocéphales*, et probablement (mais ceci par analogie seulement) de tous les autres genres de la première tribu (*Old World primates*) sont sujettes à un écoulement périodique reparaissant avec assez de régularité de mois en mois. . . . L'écoulement coïncide, chez toutes les femelles, avec un gonflement plus ou moins manifeste de la vulve et des parties environnantes. Le gonflement est médicore chez les femelles de *Guenons*, très-considérable chez les femelles de plusieurs espèces de *Macaques* et de toutes les espèces de *Cynocéphales*. Chez tous ces derniers le gonflement s'étend, non-seulement jusqu'à l'anus mais bien au delà, et il est tellement marqué, que cet orifice se trouve alors comme environné d'un large bourrelet. La peau devient en même temps très-colorée en rouge." In 1906 Pocock gave a list of those primate species which in his experience of the London Zoological Gardens exhibited external cyclical changes, and in 1925 again referred briefly to the external cyclical changes. So far as I know, these two papers of his are the only ones which attempt to consider these remarkable phenomena in Primates generally.

In this section I propose to discuss the facts of the cycle which are revealed by observation only. Particular attention will be paid to the occurrence of external cyclical changes.

It is convenient to employ a term to refer to that part of the body surface of monkeys which shows characteristic changes during the menstrual cycle. Langley and Sherrington (1891) called the skin which becomes flushed in *Macaca mulatta* the "sexual skin." This term has been adopted by all who have investigated the menstrual cycle of this animal experimentally. It is both short and, in a sense, self-explanatory. It is therefore perhaps permissible to extend it to refer to other primate species which show external changes, even though such changes differ from those manifested by *Macaca mulatta*. In this paper it will be employed to indicate those parts, adjacent to the external genital organs, which show characteristic external cyclical changes during the menstrual cycle.

Old World Monkeys.

Family PONGIDÆ.

Gorilla.—Adult female gorillas have been kept in captivity, but no record of the gorilla menstrual cycle is available. Grabowsky (1904 and 1906) (quoted by Yerkes, 1929) reports periodic sexual excitement in an immature specimen. A female observed by Yerkes (1928) died when about seven years old. She had shown no signs of reproductive activity, and no periodicity was noted in her sexual behaviour.

Chimpanzee.—In 1844 Savage and Wyman reported on the external characters of four chimpanzees, two of which were females. The descriptions of both these females are of interest. The first, whose canines had not completely erupted, was in the early stages of pregnancy. "The vulva and anus were surrounded by thick, flabby folds of skin of a light dingy yellow, which were very protuberant." The second, considered to be a very aged specimen, had with her when she was shot two young chimpanzees, and it was possible to squeeze milk from her breasts. In this beast, too, the vulva and anus were surrounded by thick and very protuberant folds of yellowish skin, forming "an elastic cushion."

Ehlers (1881) quotes a letter he received from Bolau, who had kept an adult female chimpanzee. This animal manifested reproductive activity during the two years preceding her death, undergoing approximately four-weekly menstrual cycles. The bleeding was followed by swelling around the external genitalia and anus. At first the swelling disappeared between each menstrual process, but

gradually the amount of swelling became greater at each cycle, and finally never completely disappeared in the intervals between the menstrual discharges. The time relation of the swelling to the catemenia was not noted. Bolau was of opinion that the extraordinary amount of swelling shown by this animal was possibly due in part to what he called her "unbefriedigte Geschlechtstrieb." Ehlers disagreed with this opinion on the strength of Savage and Wyman's descriptions.

According to Keith (1899), "for six to eight days before the discharge appears" the female chimpanzee is "in heat, the genital labia are turgid and swollen, the nipples are fuller and more erect. When the discharge appears, the state of turgescence in the pudendal organs passes away." This information was supplied to Keith by a keeper in the London Zoological Gardens.

Montané (1915) refers indirectly to the hypertrophy of the "sexual skin" during the cycle when discussing the pregnancy of a certain female chimpanzee. Pregnancy was suspected "from the fact that the genital turgescence was moderated at the same time that the amount of bloody issue was diminished,—when it was known that, at these periods, the development of the external genitalia usually reaches an enormous size" (Bingham's translation, 1928).

Sokolowsky (1923) gives an illustration of the swelling of an adult chimpanzee, and states that it occurs before the menstrual flow.

Köhler (1927) provides the clearest description of the chimpanzee cycle. He writes that "the female of the species definitely menstruates, at intervals of thirty to thirty-one days, and always for a period of between three and six weeks (*sic*!)*. During the flow her sexual instinct is absolutely quiescent, but her temper is often particularly amiable. After the cessation of the flow, there is an access of sexual desire, accompanied by an enormous swelling around the genitalia. At this time the animals are irritable and uncertain in temper, and suffer a good deal from the very sensitive swollen area until it subsides." It is unfortunate that Köhler did not note when the subsidence occurs in relation to the succeeding catamenia. His reference to the swelling as being painful is interesting, as the similar swelling in other genera appears to be no more sensitive than any other skin area.

Reference to the chimpanzee cycle, unfortunately without details, is found in a paper by Fox (1929). Vaginal bleeding was observed in a female chimpanzee eleven days after parturition. "Thirteen days after delivery, there was definite swelling of the whole perineal region, as if the period were returning.... Swelling remained at the height for four days, but there was no true menstrual flow except the one day mentioned above, although the external appearance was that of normal menstruation. The swelling subsided at the usual rate." Fox would seem to be under the impression that, in his chimpanzee, bleeding accompanies activity of the sexual skin. If this is true it is somewhat remarkable, for the two phenomena have always been described as occurring at different times of the cycle, not only in chimpanzees, but in all primate species which show cyclical activity of the sexual skin.

Orang-utan.—The only reference of any value to the reproductive mechanisms of the Orang that I know is contained in the paper by Fox, just quoted. As it concerns pregnancy it has been included in Section VIII. p. 733.

Family HYLOBATIDÆ.

Gibbon.—Little information about the Gibbon is available. According to Pocock (1905), the Hainan Gibbon (*Hylobates hainanus*) becomes sexually mature at seven years. A female of this species was observed for about nine months, and Pocock states that "in Gibbons the interval between the menstrual discharges is

* Obviously, "weeks" should be "days."

a little over the calendar month, and that the discharge continues for two to three days." "The pudendal organs are always conspicuous by reason of their turgescence, and no very conspicuous change in their condition precedes the menstrual discharge."

One adult female specimen of this family, a Siamang, *Symphangylus syndactylus*, has been closely observed for many months, but neither menstruation nor any variation in the conformation of her perineal region (which is not prominent) has been noticed. The same remarks apply to an adult female *Hylobates lar*.

It might be noted in passing that there is probably less sexual dimorphism in Hylobatidæ than in any other primate family. Field workers, and even systematic zoologists, frequently experience difficulty in distinguishing the two sexes. The lack of cyclical variation in perineal form probably adds greatly to this difficulty.

Family Cercopithecidæ.

Genus Pithecus.

Very little appears to be known about the reproductive activity of this genus, and Heape's monograph, "The Menstruation of *Semnopithecus entellus*" (1894), remains almost the only source of information. "The external phenomena attending menstruation in *S. entellus* is marked by the discharge which flows from the vagina during about four days each month. Unlike *M. rhesus*, there is no vivid colouring of the buttocks, stomach, thighs, or tail, and the only other external sign of menstruation is a slight swelling of the vulva, and, sometimes, of the nipples of the mammæ." I do not know of any other reference to the cycle in Langurs, or *Nasalis* monkeys, or their African cousins, members of the genus *Colobus*.

For a period of three months I have had under observation an adult female of the genus *Pithecus*. The pudendum of this animal is turgid and prominent, but I have been unable to observe any variation in its size. Moreover, Mr. Goodfellow, in whose care the animal has been for some months, tells me that he has never noticed any cyclical changes.

Genera Cercopithecus and Erythrocebus.

Genus *Cercopithecus* includes the African tree-monkeys, and contains a larger number of distinct species than any other primate genus. Genus *Erythrocebus* is closely related, and contains a few species of a more terrestrial group of monkeys.

In almost all the species of these two genera thus far observed the only external sign of the cycle would appear to be the catamenia itself, no cyclical variation in the conformation or coloration of the perinæum occurring. Pocock remarked on this in 1906, and again in 1925 he writes that no "trace" of these changes is ever observable in *Cercopithecus* or *Erythrocebus*.

I have had under observation in the Zoological Society's Gardens about thirty adult females of species belonging to these genera. With the exception of one, *Cercopithecus talapoin* (discussed below), I too have been unable to recognize any external cyclical changes. In most females belonging to these genera the perinæum is obscured by hair, and the external genitalia are accordingly inconspicuous, so that, unless the examination is closely carried out, the menstrual process itself passes unnoticed. One female not on exhibition, belonging to the species *Cercopithecus æthiops*, has been closely observed daily, but no appreciable variation in the prominence of the external genitalia or the surrounding skin has been noticed. She undergoes regular cycles averaging 31 days, bleeding lasting about two days.

In his 1925 paper Pocock notes that the external generative organs of the

female *Cercopithecus* are "usually small and inconspicuous, but in an adult example of *C. talapoin* there was a tolerably long pendulous clitoris projecting below the edge of the callosities like a short penis, and recalling the condition seen in some South American monkeys, e. g. *Cebus*. *C. talapoin* is the smallest of all the species of *Cercopithecus*, and it retains, in the skull at all events, certain characters found in immature specimens of the larger species. In this connection the length of the clitoris, probably a primitive character, is interesting."

Cercopithecus talapoin, however, differs far more strikingly than this from the other members of its genus. It exhibits external cyclical changes.

An adult female of this rare species has been under close observation for the greater part of a year. Although she is a caged animal and therefore not handled, her perineal area is easily seen, because it differs from that of other species of *Cercopithecus* in being relatively hairless and more truncated, as in *Papio*. At no time has she been seen to menstruate. It is possible, however, that bleeding is so slight that it may have been missed. When quiescent, the pudendal organs are inconspicuous, the clitoris pointing backwards. When the sexual skin it active, the clitoris and the skin surrounding it swell out into a subpubic lobe about an inch in diameter. The skin of the labia majora and the skin adjacent, as far laterally as the callosities, and posteriorly including the skin as far back as the base of the tail, swell into a series of folds. The colour of the sexual skin is the same in the inactive as in the active stage. The change from the quiescent to the hypertrophied state and the return to the resting stage are slow.

During the period of observation, five irregular cycles of activity of the sexual skin have been noted.

Genus Cercocebus.

In the mangabeys cyclical coloration and hypertrophy of the sexual skin are very marked. Pocock (1906) noted the phenomenon in the species *fuliginosus*, *torquatus* (= *lunulatus*), and *collaris* (= *æthiopicus*). In 1925 he described the swelling in *Cercocebus* as of "moderate size, and constant in form in all the species observed. It consists of an upper and a lower rounded expansion united by a narrower area, and extends from the root of the tail above to the clitoris below. Its upper and lower edges are evenly convex above and below the callosities, and its lateral margins are deeply and widely concave where they abut against the inner extremities of the callosities, which fit into the hollows, thus causing the constriction in the swelling. The upper lobe is developed round the anus, the median portion round the vulva, and the lower portion round the clitoris, this portion apparently resulting from an expansion of the preputial glandular sheath of the clitoris. The groove between the vulva and the clitoris is entirely obliterated, and the clitoris itself appears as a small bilobed excrescence above the orifice of a glandular pit in the centre of this part of the swelling." In neither of these two papers does Pocock note the time relations of the perineal swelling to the catamenia.

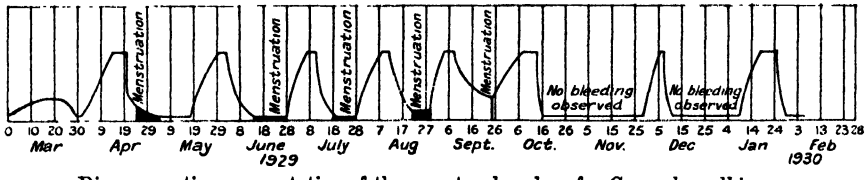
I am indebted to Miss Hume, of the Lister Institute, for the following information about a Sooty Mangabey (*Cercocebus fuliginosus*) which was under treatment for rickets.

This mangabey arrived at the institute on the 26th of February, 1926, in the process of shedding its milk teeth, and weighing at that time 2920 gms. Towards the end of April hypertrophy of the sexual skin was noted for the first time. Maximum growth was slowly reached, and persisted until the first week in June, when absorption of the swelling took place. Menstruation followed about a week later, lasting a week, and its termination was immediately succeeded by perineal hypertrophy. The beginning of absorption of the swelling occurred 20 days after the onset of the preceding catamenia, and was followed by the menstrual bleeding after 6 days, bleeding on this occasion persisting for 8 days. As before,

the end of the catamenia coincided with the beginning of perineal hypertrophy. Five cycles in all were observed before the animal's death, of average duration thirty days, varying from 26–33 days. Bleeding was always prolonged, the perineal swelling beginning at its termination and diminishing about the middle of the cycle. At its death the animal weighed 3795 gms.

There is only one sexually mature female mangabey at present living in the Society's Gardens, a female of unknown age belonging to the species *Albigena*, that was presented in October 1926. Her sexual maturity, however, dates only from March of 1929, and up to the present her menstrual cycles have been irregular. Slight swelling of the labia majora was the first sign of reproductive activity; this subsided towards the end of March, the external generative organs resuming their inconspicuous resting level above that of the lower surface of the callosities. The sexual skin, the extent of which is indicated in Pocock's description of the swelling (given above), became active again in the first week of April, and in fourteen days from the commencement of swelling the appearance of the perinæum corresponded in all details to the description which, according to Pocock, applies to all species of *Cercocebus*. The approximate dimensions of the swelling

Chart 1.



Diagrammatic representation of the menstrual cycles of a *Cercocebus albigena*.

See Explanation of Charts, p. 754.

at this time were: 4 inches in length (from base of tail to anterior limit of clitoric swelling), 2½ inches in width (at widest part), and 2 inches in depth. These dimensions have not been surpassed in any of the cycles which have followed. A thin discharge (non-sanguineous) flowed during the time the swelling persisted. After remaining at its height for five days the swelling rapidly dwindled, and within three days the labia majora just projected beyond the level of the lower surface of the callosities. They resumed their quiescent position a fortnight later.

No bleeding intervened between the slight swelling in March and the swelling in April. Bleeding began four days after the subsidence of the April swelling, and lasted ten days. As in almost all monkeys, external bleeding in this mangabey is neither profuse nor continuous; the intravaginal opening of the urethra provides a means whereby the vaginal contents are periodically washed out.

The later cycles of this animal have been correspondingly irregular, and bleeding has frequently been of long duration. Whereas the May swelling started fourteen days after the cessation of the bleeding which followed the April swelling, the July swelling commenced only two days after the cessation of the June bleeding. No external bleeding occurred between the October and December swellings, and between the December and January swellings. The cause or causes underlying these irregularities are not known. Probably the youth of the animal is in some way a factor. The complete record of this animal's cycles is given in Chart 1.

Genus Macaca.

Macaca mulatta (= Macacus rhesus).

More has been written about the reproductive mechanisms of this animal than about those of the rest of the primates put together.

Heape (1896) writes that the menstrual flow of this monkey is associated with "a congestion of the skin of the abdomen, legs, and tail, a swelling and congestion of the nipples and vulva, and flushing of the face." The time relations of the sexual skin activity to the flow are not recorded.

Pocock in both 1906 and 1925, when drawing attention to the external cyclical phenomena associated with the menstrual process in primates, confined himself almost entirely to the swelling of the sexual skin. In both his papers he states that swelling does not occur in *M. mulatta*. In 1906 he writes that he "never detected it in Macaques (*Macacus*) of the Common (*fascicularis* = *cynomolgos*), Bonnet (*sinicus*), Rhesus (*rhesus*), and Japanese (*fuscatus*) species"—an opinion he reaffirmed more strongly in 1925.

It will be found that descriptions of the external changes in *M. mulatta* are somewhat conflicting, and that they are all characterized by lack of detail regarding the time relations of sexual skin activity to menstruation. This is doubtless due to the absence of marked swelling. Without any objective colorimetric standard it is almost impossible to be sure that the colour of the sexual skin is more intense one day than another.

Collings (1926) provides a detailed description of the sexual skin in *M. mulatta*, which I quote here in full.

The sexual skin "is not limited to the immediate vicinity of the anal and vaginal orifices, but extends a few centimetres out on the underside of the tail and forward a bit on the lower abdominal wall. It also spreads well out over the buttocks and well down on the backs and insides of the thighs. The areas are quite symmetrical in arrangement. The border-line is quite sharp and clear-cut, and does not change in its location from the earliest blush to the very height of color. The color is red, but often has a peculiar bluish tinge similar to that of a cyanosis. The hair of the area is rather sparse in distribution, but, when the phenomenon is at its height, stands out erect and bristling. This state of hair erection develops and wanes very gradually, usually lasting some three to five days. The configuration of the 'sexual skin' varies through the cycle. During the stage of least coloration and in spayed animals it resembles the surrounding integument, except that it is more roughened, like 'goose flesh.' With medium coloration the 'sexual skin' appears smooth and tense, but upon closer examination it is found not to be tense in the true sense. Later, when the color is at its peak, the skin becomes pouchy and furrowed with a surface sometimes closely resembling the 'orange-peel' skin found over certain tumors of the human breast. It is during this latter stage that the local hair erection, described above, occurs. During all stages the 'sexual skin' is of medium texture and has a greater elasticity than the rest of the integument. No suggestion of œdematous pitting was noted at any stage of the process, with one exception. This was in the case of a spayed monkey that had become very red and pouched under the influence of sex-hormone injections. The slight pitting in this case was not general, but localized to an area in the midline just anterior to the vaginal orifice."

In my experience the actual amount of body surface that shows cyclical coloration varies from female to female in the species, and in the same animal from cycle to cycle. Swelling and pouching of the sexual skin is not obvious in all animals. Some females develop at the height of coloration pronounced rugous swellings on the antero-lateral aspects of the thighs. Such swellings appear gradually in the earlier part of the cycle and disappear with greater rapidity about the middle. In others the dorsum of the base of the tail is affected. In one I observed swelling of the vulval lips and anus.

Corner (1923 *b*) found that the menstrual cycle of *Macaca mulatta* varied "about a modal length of 27 days," the menstrual flow lasting from 4 to 6 days. In his experimental colony "it happened that all the intervals of excessive length (over 50 days), with two exceptions, occurred between June and January. Accord-

ingly, there appeared to be a tendency to greater regularity of the menses in the late winter and spring." Corner made an especial effort to note any relationship between the menstrual cycle and cyclical coloration. His conclusion is that coloration "fluctuated, as to presence and extent, in a very capricious manner Once established, it sometimes persisted throughout several cycles, and at other times disappeared almost entirely after the menstrual flow. Once or twice, one day's time was sufficient to accomplish complete fading of the pigmentation and to reduce the inguinal pouches from the size of walnuts down to a few flabby folds of bluish skin."

Collings (1926), however, found that the coloration of the sexual skin of *M. mulatta* "reaches its apex during the third week after the onset of menstruation and fades gradually as the time of the next menses approached." Allen (1927) also noticed that the cyclical coloration was most marked between the tenth and twentieth days of the cycle, which in his monkeys averaged 39 days. The waning of the sexual colour was taken as a sign of approaching menstruation.

Hartman (1927, *et seq.*) has added considerably to our knowledge of the reproductive history of this species of monkey. Puberty, which he considers to occur at four years of age, is indicated by menstruation, sexual coloration, and the appearance of "bag-like swellings" in the pubic region. "The swellings of puberty are usually confined to the region corresponding to the scrotum of the male, and may well be homologised with it." "The menstrual cycles of the younger monkeys are usually much more irregular and unreliable than those of older females, both in the length of the interval and the duration of the flow." Hartman also records prolonged periods of summer amenorrhea in several of his animals (see his later records, p. 694 above). After referring to the swelling and coloration that occurs in the adolescent female, he writes that older females "sometimes do show a swelling and edema, occasionally almost pathological in extent, over the buttocks, the hips, and the base of the tail—parts that redden, especially in the interval of the menstrual cycle. These swellings are rare, however, and quite a different thing from the more localized pubic swellings of adolescence." In a footnote Hartman mentions that swellings over the whole sexual skin "occur in not over one-fourth" of adult females, "and in these it occurs only occasionally" (1928 *e*).

I am greatly indebted to Dr. C. Dobell, F.R.S., of the National Institute for Medical Research, Hampstead, London, for the following history of a rhesus macaque, who first menstruated on the 3rd of March, 1928, after she had been $1\frac{1}{2}$ years in England. Her weight at this time was 3300 gms. At first she was irregular. Reddening and "quilting" of the thighs and abdomen first appeared in the month preceding menstruation. The "quilting" has persisted ever since, but becomes most pronounced midway between the periods. It varies from time to time in extent. In 1928 this female menstruated only 3 times (3. 3. 28; 17. 8. 28; 8. 10. 28). In the interval between the first and second of these occasions the "quilting" extended above the umbilicus and down to her heels. At the same time her face became very red, and she had a very large red interorbital swelling. The fourth time this female menstruated was 2. 2. 29. Since that date and up to the present (Jan. 20, 1930) she has menstruated 12 times. The average length of these 12 cycles has been 28·3 days, the range of variation being 23-41 days (see Chart 2).

Macaca radiata.

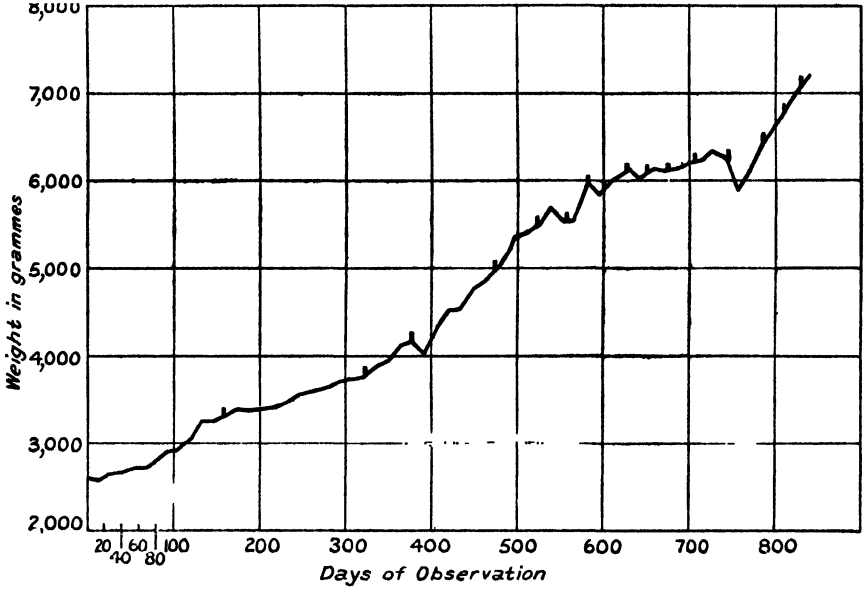
The Bonnet Monkey of India, common though it is, has not, up to the present, attracted the attention it deserves. It presents certain unusual features.

Percy in 1844, in a paper on the management of monkeys in captivity drew attention to one of its more obvious peculiarities. He writes: "two

individuals of *Cercopithecus radiatus* (= *Macaca radiata*) are habitually affected with a copious discharge from the vagina. I have sometimes seen large, transparent, colourless clots of mucus evacuated." This, so far as I know, is the only published record of the mucous discharge of the Bonnet Monkey, though it is well known to all who have kept the species. I do not know of any record of the anatomical condition responsible for the phenomenon.

The death of a *Macaca radiata* in the London Zoological Gardens this year provided me with the opportunity of investigating the cause of the discharge. I found that the cervix is unusually large, and that its mucous membrane is thrown into a large number of folds, supported by a central stroma, from which bud off

Chart 2.



Growth curve of a *Macaca mulatta* (= *Macacus rhesus*) over a period of 840 days, on which are marked the times of menstruation. This chart is a record of puberty. The first day of observation was the 28th of September, 1927.

100=6-1-28. 200=15-4-28. 300=24-7-28. 400=1-11-28.
500=9-2-29. 600=20-5-29. 700=28-8-29. 800=6-12-29.

Data from Dr. C. Dobell, F.R.S.

secondary folds which again branch. The folding is very complex. The lining epithelium is composed of large glandular cells which also line the glands which dip in all directions (see Pl. I.). A fuller description of the histological features of the internal generative organs of this animal will appear in a future publication.

Pocock in 1906 remarked on the absence of cyclical phenomena in this animal, which in his experience did not menstruate in captivity. He mentions, however, that a female of this species kept by Dr. Hamish Nicol did menstruate, and menstruation had also been observed earlier by Percy (1844).

For about a year I have closely watched three female *Macaca radiata* in confinement in the London Zoological Gardens *.

In one of them menstruation was observed in four consecutive months, the cycle lengths being 31, 33, and 29 days. Bleeding has been observed only once in each of the other two. Unfortunately, observation in this species is made difficult because of the heavy mucous discharge.

The pudendal area of *Macaca radiata* is coloured a deep purple, and the face, too, is frequently highly coloured, or pigmented in red patches. No cyclical swelling of the sexual skin occurs, and it is almost impossible to tell whether there is any variation in colour during the cycle.

In the animal which menstruated four times it seemed that the secretion of mucus was most profuse towards the middle of the cycle, diminishing as the menses approached. In the second the mucus has been continuously profuse, while in the third the amount fluctuates from day to day, and is absent for several days at a stretch.

I am indebted to Dr. C. Dobell for the following data regarding a female *Macaca radiata* in his possession. Dates of menstruation in 1926 were Jan. 8–11, Feb. 15 (continuing intermittently to the 25th), and March 20–27. She did not definitely menstruate again in 1926, though at irregular intervals an occasional streak of blood was found in the vaginal mucus. The monkey became pregnant in September, giving birth to a still-born baby on the 26th of February, 1927. Her first menstruation after this was on April 17th, then on May 15th, July 9th, August 14th, and October 28th.

The intervals between May 15th and July 9th, and between August 14th and October 28th, are each suspiciously near the length of two cycles. Assuming this to have been the case, the average cycle length in this animal is 33 days. Disregarding this possibility, the average is 44 days.

Macaca irus.

This is the Common Macaque, which has a wide distribution in South-East Asia, Burma, Siam, and the Malay Peninsula and islands. It was studied under the name of *Cercocebus cynomolgos* by Van Herwerden in 1906.

Pocock in both 1906 and 1925 remarked on the absence of cyclical coloration in this species. Apart from this negative statement, I do not know of any reference to the cycle of this monkey.

For about a year I have kept adult females of this species under observation. Unfortunately they are caged, and, as I have previously noted, it is impossible under such circumstances to be certain that one has not overlooked menstruation. With two exceptions (in one I have seen fairly regular bleeding in the past six months, and in the other bleeding only once), my experience has been similar to Pocock's, who never observed menstruation in this species. The average of four cycles in the exceptional animal is 41 days.

Almost all females of this species, young and adult, show "scrotal" swellings similar to those described by Hartman as characteristic of puberty in *M. mulatta* (see p. 703). The swellings vary in colour from a deep black in younger animals to a yellowish pink in older animals, and vary also in prominence from one animal to another. Though I have little doubt that these swellings are homologous with the similar condition in *M. mulatta*, I have been unable to convince myself that they vary in any way during the cycle.

Many fully mature females of this species also show a swelling of the base of the tail. In some this swelling is very prominent. I have no doubt that both the amount of the swelling and the colour, which may be quite bright, vary in the

* Another female of this species arrived in the Gardens on the 6th of January, 1930. She menstruated on the 10th, and again 23 days later. Her mucous secretion is always profuse.

same animal from time to time, but thus far I have failed to note any cyclical variation, or any relationship to the menstrual process.

This type of swelling is probably the same as that described in *M. cyclopis* by Sclater in 1864 and Murie in 1872. I have not seen swelling of the tail in any species of Macaque other than *Irus*, though Anderson (1878) affirms that he has seen tail-swelling in "*Macacus rhesus*." His observation, however, is queried by Pocock, who believes it was not the animal now known as *Macaca mulatta*, the common Indian rhesus monkey, to which Anderson was referring, but *Macaca assamensis*, the Himalayan monkey.

MACACA NEMESTRINA.

Pocock in both his papers records the occurrence of external cyclical changes in the pig-tailed monkey, though he does not note the time relation of the swelling of the sexual skin to menstruation. He states that the change "involves the root of the tail, which is thrown into thick transverse folds, and the whole of the naked area of the rump all round the anus, the genitalia, and the callosities are affected, and its red colour intensified" (1925).

There is only one adult female of this species at present living in the Zoological Society's collection. She has been under close observation ever since she gave birth to a male baby on July 15th, 1928. It was not until March of 1929 that she showed signs of physiological activity of the generative tract, though secretion of milk had probably ceased before this. (Her baby continued to suck, but did not seem to draw milk.) In the first week of March her sexual skin commenced to brighten in colour and to swell, and this continued, the colour varying in intensity and the swelling in extent until the last week in April, when the swelling became relatively enormous and blue-red in colour. No greater activity of the sexual skin has been observed since.

Her appearance at this stage differs somewhat from that described by Pocock. She shows very little tail swelling. The skin anterior to the pudendal cleft swells into an elongated pubic lobe which includes the clitoris. The anterior lobe may be divided by a transverse groove into two parts. The anterior limit of this part of the swelling is concealed slightly by abdominal hair. The pudendal margins and the skin surrounding the anus swell into a prominent, smooth, blue-red anal pad which extends laterally around the callosities, which are not affected and are not covered. No appreciable change occurs in the colour of her nipples or face.

The swelling began to disappear and the colour to fade on the 30th of April, and within a week her perineal area had resumed its quiescent state. Menstruation started on the 15th of May, lasting four days. On the last day of bleeding her sexual skin again showed signs of activity, reaching its limit of swelling and coloration on the 30th of May. It remained at its height for about four days from this date, the swelling disappearing completely during the 4th of June. Menstruation started fifteen days later, June 19th, and lasted two days.

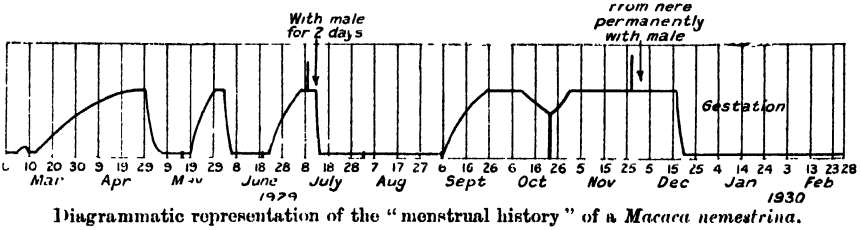
The second cycle therefore lasted 35 days. Her third cycle, which lasted 44 days, began with swelling of the sexual skin immediately after the second bleeding ceased; swelling gradually reached its maximum, and disappeared suddenly on the 24th day. Menstruation commenced 20 days later. She was mated with her male on the 20th and 21st days of this cycle without success. The next (4th) cycle of 34 days was remarkable, as swelling and coloration of the sexual skin were almost imperceptible. The terminating menstruation was, however, normal. The one following (5th) was the reverse, in so far as the sexual skin remained swollen throughout a cycle that lasted 47 days. The succeeding cycle was also different, for the maximum height of the swelling was maintained for almost 50 days before it suddenly subsided. Her male was

reintroduced to her on the 36th day of this cycle, and has been allowed to remain. Subsidence of swelling occurred 20 days after his introduction. They have mated frequently, and as over 50 days have elapsed since the last subsidence of swelling without the appearance of menstruation or external change, it is almost certain that she is again pregnant (see Chart 3).

MACACA FUSCATA.

The Japanese Monkey is the only other adult female macaque which I have had the opportunity of observing, and, like Pocock, I have observed neither menstrual bleeding nor external cyclical changes. The animal's normal coloration, both of face and perineal area, is a very bright red. Owing to the difficulty attending observation of this specimen, I am unable to state definitely that cyclical changes do not occur.

Chart 3.



Diagrammatic representation of the "menstrual history" of a *Macaca nemestrina*.

See explanation of Charts, p. 754.

MACACA CYCLOPIS.

Murie (1872) gives a quaint description of the cyclical swelling in this monkey, which is figured by Sclater (1864). He writes that "in the female Rhesus Monkeys and the Baboons, at stated periods the hinder parts become unusually florid and puffy, but generally speaking the tumidity is restricted within reasonable bounds. In the case of the Round-faced Monkey, however, not only are the callosities and external genitalia swollen, but even the proximal end of the tail is inordinately increased in dimensions. In short, the whole of the posterior parts are literally a mass of deformity. The skin and subcutaneous tissues are frightfully distended, purple, deep red, and roseate, and here and there bagged out in great folds as if they were ready to burst from sanguineous and serous effusion. It is a hideous spectacle!"

MACACA SYLVANA.

According to Pocock the sexual skin of the Gibraltar Ape becomes turgid and slaty or purplish in tint. "In the female of this species the region of the rump above the anus rises into a high dome-shaped expansion, so that there is a long area between the anus and the generally externally invisible tail."

MACACA MAURUS.

Pocock believes similar changes occur as in *Macaca sylvana*.

MACACA SILENUS.

Pocock writes that in dried skins of this species "there is a large area of naked integument above the anus and callosities and a moderately wide area external to them, and in living examples these areas are greatly swollen, the upper area

forming a great cushion-like transverse expansion which lifts the base of the tail into a vertical position." Pocock believes that similar changes occur in *Macaca lasiotis*.

I do not know of any statements regarding other species of *macaca*.

Genus Cynopithecus.

Pocock writes that the swelling in *Cynopithecus niger* affects "principally the lateral area of the rump, where it is widely extended, lobate, and folded. The base of the tail is involved only to a small extent in the specimen examined; the anal eminence and the vulva are not affected, but retain their normal position and form, lying in a groove formed by the expansion of the tissues on each side of them. The area round the callosities on each side of the vulva, however, overlap and conceal it, and have to be pulled aside for its exposure; but the swellings do not extend ventrally below its inferior end, and the preputial sheath is unaffected. So far as my observations go the swelling in this genus conforms in a general way to that characteristic of some species of *Macaca*, and is different from that of *Papio*" (1925).

I myself have not had the opportunity of observing an adult female of this genus.

Genus Theropithecus.

I have no personal knowledge of the female of this interesting genus, nor had Pocock, but, on the testimony of keepers in the Zoological Gardens of London, Pocock writes that there is no cyclical variation in the condition of the genitalia or adjoining sexual skin, both of which are normally somewhat turgid and prominent. In the species *Theropithecus gelada*, however, there exists in both male and female a bare spot on the chest and neck which is very brightly coloured. "The patch may be described as composed of two triangles reversely directed with their apices close together or confluent. . . . In the female where the two triangles are confluent, the shape of the patch may be likened to that of an hour-glass, and in this sex the patch is, as Garrod said, carunculated all along its lateral and inferior borders. These caruncles are ovate, flattened, and numerous, and, as I have been informed by Shelley, the keeper in charge of an adult pair of these animals recently exhibited in the Gardens, become enlarged during menstruation. *Theropithecus* is unique in the Cynomorpha in possessing this pectoral patch" (1925).

Genera Papio and Mandrillus.

These two genera may be considered together, as their external manifestations of the cycle are alike.

Pocock in 1906 described the cyclical changes in *Papio porcarius*, *Papio papio* (=*Papio sphinx*), *Papio anubis* (=*Papio olivaceus*), *Papio hamadryas*, and *Papio cynocephalus*. "The period of 'heat' is heralded by inflammation of the genito-anal area and is followed after a day or two by a flow of blood which continues for four or five days, during which time the inflammatory swelling gradually increases in size. . . . After the hæmorrhage stops, the swelling continues to grow and extends laterally so as to conceal completely the ischial callosities and the naked skin adjacent. It reaches its maximum in about two weeks' time and remains at that stage for about one week. It then begins to shrink, and in about another two weeks has disappeared, so that the female at a distance is indistinguishable from the male. After a few days' rest inflammation again sets in and is almost at once followed by the appearance of hæmorrhage." Pocock noted that the cycle is monthly and that individual variation exists in the amount of blood lost. In

1925 he extended the observation to the genus *Mandrillus*, and also recorded the fact that external changes are most marked in *Papio porcarius*.

Gear's description of the cycle in *Papio porcarius* (1926) is remarkable. It is Pocock's description reversed.

He writes, "the length of the œstrous cycle in the baboon . . . is 34·6 days, that is, a rhythm of five weeks. . . . From an examination of the external changes alone, it is possible to divide this cycle into definite periods corresponding with similar periods in other mammals, as noted for instance by Hartman (1923) in the opossum, Allen (1923) in the mouse, and Corner (1921) in the sow.

"The cycle is divisible into: (1) the diœstrous interval, a period of rest; (2) the pro-œstrous, when the genitalia undergo great morphological changes; (3) œstrous, the period of sexual desire; (4) metœstrous, when the processes of degeneration in the genitalia occur.

"In the baboon the diœstrous period averages ten days, and, during this time, the pudendum is in no way conspicuous, the labia majora appearing merely as two narrow longitudinal folds of wrinkled scaly skin, between the ischial tuberosities. The diœstrous period terminates in the occurrence of very remarkable changes in the external genitalia. In a few days, usually four, the labia majoria, the clitoris, and the anal mucous membrane hypertrophy to a great extent. At the height of this growth there is a huge spherical swelling around the anus, entirely covering the gluteal region, and, extending downwards and forwards from this swelling, is the similarly enlarged vulva. The size of the organs reached at each œstrous period is approximately the same for one individual, but in different animals there are variations. Nevertheless, in the least pronounced enlargement the following measurements were obtained: Transverse diameter of spherical swelling, 10 inches; depth of swelling, 5 inches; length of vulva, 8 inches; breadth of vulva, 4 inches.

"Other measurements in other animals were greater by three or four inches in the diameter of the anal swelling. This enlarged anal swelling is usually irregularly lobulated, the lobules being rounded and smooth of surface, the whole giving the impression of great vascular tension. The pudendal swelling is of a similar appearance and nature, although not lobulated. The colour is a vivid, glistening red, approaching almost the depth of beetroot red.

"This exaggerated appearance continues for some time, averaging nine days, associated with obvious changes in the animal's behaviour, demonstrating sexual desire. Often there appear fissures, cuts, and abrasions on these organs as the period lengthens. These injuries show hæmorrhage, serous exudation and usually a small amount of suppuration. However, the enlarged area seems in no way ultra-sensitive, as the baboons in this condition do not hesitate to adopt sitting postures in which the external genitalia are brought into severe contact with such hard objects as rough wooden boxes. Though the change in the tissue may be analogous to an inflammatory condition, yet it evidently does not result in inflammation.

"Throughout both the pro-œstrus and the œstrus there occurs an excessive vaginal secretion, which varies in character from a thick white, viscid, mucoid secretion during pro-œstrus to a more serous, watery secretion during the later stages of œstrus.

"In the nipples there is a synchronous change in size and colour. They become slightly tense, losing their usual scaliness and wrinkled appearance. The colour also deepens, resulting in a tinge of red in the nipple.

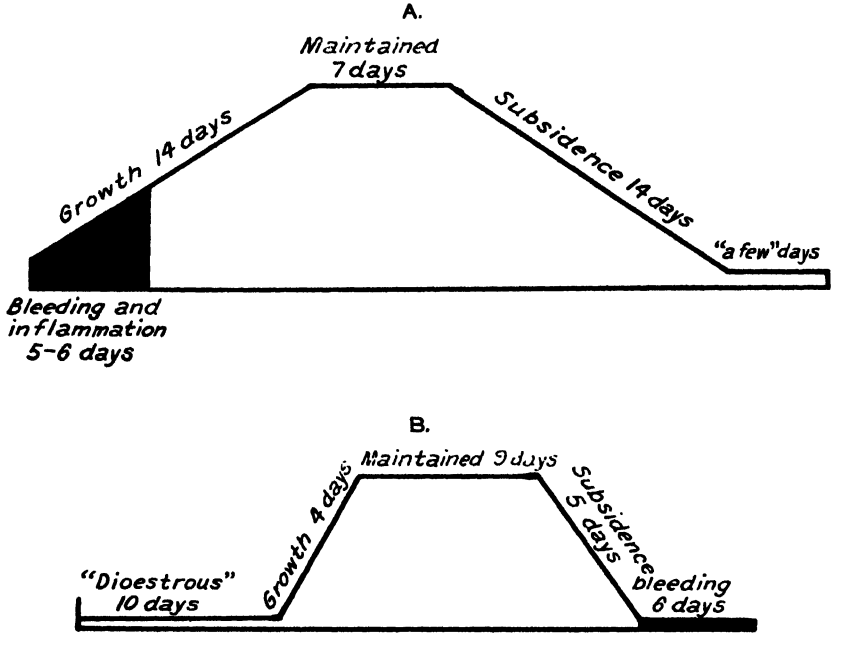
"There is evidence, in these external enlarged organs and in the increased vaginal secretion, of similar associated hypertrophic changes occurring in the vagina and uterus. As has been mentioned before, these relations are probably provoked by ovarian hormones.

"With startling rapidity the hugh swellings subside. There appears first a scaliness and loss of glistening effect and colour, the smooth surface rapidly

wrinkling and shrinking, so that, within five days, the anal and pudendal margins are once more their normal resting size and appearance. This return to normal is followed at once or within two days by a slight vaginal flow of blood and serous fluid, and this menstruation evidently represents the metœstrus, during which the hypertrophied mucous membrane of the genital tract undergoes degeneration and desquamation. This blood-stained flow continues for an average of six days, and then once more the diœstrous period follows."

There is a striking difference between Gear's and Pocock's descriptions. According to Gear, a quiescent interval of ten days elapses between the menstrual bleeding and the beginning of hypertrophy of the sexual skin. According to Pocock, hypertrophy b gins during the bleeding, and reaches its maximum in about fourteen days (see Diagram 1.).

Diagram 1.



The Menstrual Cycle of *Papio porcarius*. A. According to Pocock. B. According to Gear. The curve represents swelling of the sexual skin.

Before recording my own observations on this genus, Distant's (1897) record of nine cycles in a specimen of *P. porcarius* may be noted. The average cycle length was 41 days, the range of variation being 34-67. Percy (1844) left a record of the cycle in the drill. He writes: "I have a *Papio leucophœus* (=*Mandrillus leucophœus*), which I have had for four years, which regularly, so far as I have observed, menstruates at intervals of about six weeks. The labia become enormously swelled and protuberant, and during the subsidence of the swelling a sangineous discharge appears."

My own observations in these two genera have been restricted to the species *Papio hamadryas*, *Papio anubis*, and *Papio cynocephalus*.

PAPIO HAMADRYAS.

During 1929 ten adult females of the species *P. hamadryas* were under observation. Of these one (C. 12) died three months after I began observations (see Chart 4). Another was a female (M) which had given birth to a male baby in September 1928, and which died on the 31st of August, 1929. In the period following the birth of her baby she only once showed swelling of her perinæum. This did not reach the normal maximum of her species, and was not followed by menstruation. Her amenorrhea was due partly to lactation and partly to a chronic septic endometritis, discovered at autopsy.

Five of the others (Sm., Sc., Ha., Sp., Scr.) became pregnant after a few months' observation (Charts 5, 6, 7, 8, 9). In only three (Wa., Te., Gr.), therefore, have normal cycles been observed for almost a whole year (Charts 10, 11, 12).

Cycles are calculated from the onset of one menstrual flow to the onset of the next. Swelling of the vulva becomes noticeable any time during menstruation or immediately after bleeding has stopped. The duration of the catamenia has not been established with certainty, but it appears to last from 2 to 4 days. Certain of the females under observation were kept in an open enclosure, and on a few occasions bleeding was not observed. Cycles were then calculated from the onset of swelling.

The average length of 30 cycles observed in 8 of the 10 females of the species *Papio hamadryas* was 30·6 days. The cycles varied from 23–40 days. No prolonged period of amenorrhea was observed in any animal undergoing normal cycles.

Not enough cycles have been observed to establish the mode, which appears, however, to be the same as the average cycle length, *i.e.* about 30 days. Individual animals appear to be fairly regular.

Swelling of the sexual skin begins either during or immediately after the catamenia, and in this species reaches its maximum in about a week. The duration of the period of growth and the amount of swelling that occurs are both somewhat variable, differing from animal to animal and occasionally in the same animal from cycle to cycle. I have never seen the swelling so well developed in this species as I have in *Papio cynocephalus*, which again, according to Pocock, does not show as much swelling as does *Papio porcarius*. Gear's description of the size of the swelling in this species has been quoted. A striking illustration of the swelling is given by Friedenthal (1908).

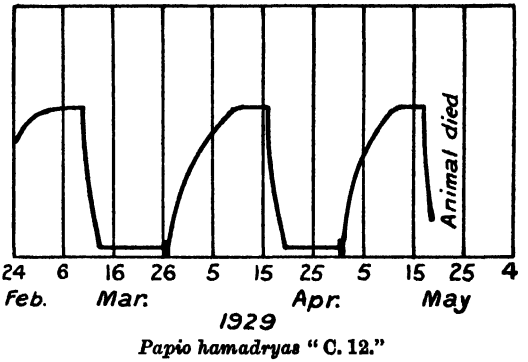
The swelling from its very beginning is demarcated into two areas; a part anterior to the middle line of the vaginal orifice (which is on a level with a line drawn through the anterior margins of the callosities), composed of the clitoris and its preputial sheath; and a posterior part composing the posterior part of the vaginal orifice and the circum-anal skin. It may be noted at this point that in the adult female of this species the vulva seldom assumes a position beneath or level with the surface of the callosities, as it does in the female before puberty. There is usually a certain amount of flabby swelling of the preputial sheath, vulval lips, and circum-anal skin, even during the quiescent phase of the cycle.

The preputial sheath swells into an oval rounded body which does not overlap its attached base. Its anterior extremity passes forwards below and anterior to the symphysis, and is covered with abdominal hair. The tip of the clitoris is generally seen in a depression near the vaginal orifice. Occasionally it is prominent.

The posterior swelling soon overlaps its attached base, which passes medial to the callosities and just anterior to the base of the tail. The ischial callosities are completely hidden. The peri-anal swelling is several times larger than the clitoric swelling. The anus has a central opening in the form of a transverse groove,

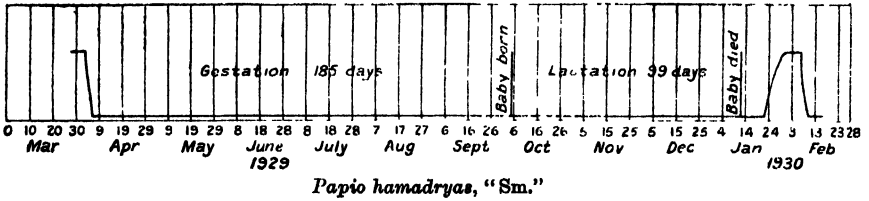
usually furrowed radially. The vaginal orifice is between the clitoris and anal swellings. Smaller grooves occasionally appear in the peri-anal swelling, producing an appearance of lobulation. The lateral part of the peri-anal swelling expands last. The swellings are very turgid and shiny, and are bright red in colour.

Chart 4.



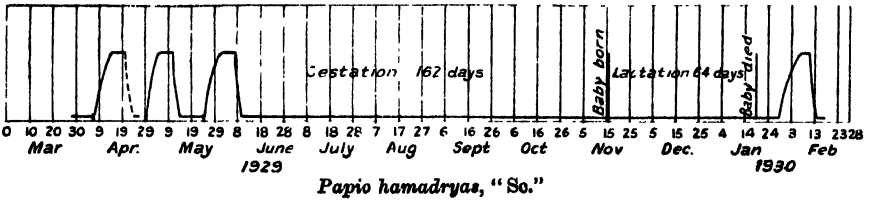
Papio hamadryas "C. 12."

Chart 5.



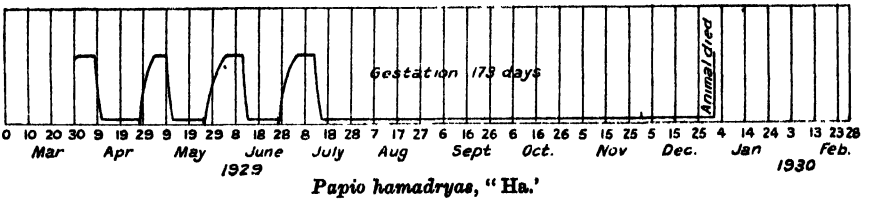
Papio hamadryas, "Sm."

Chart 6.



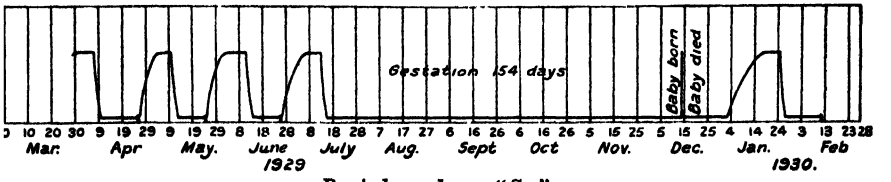
Papio hamadryas, "So."

Chart 7.



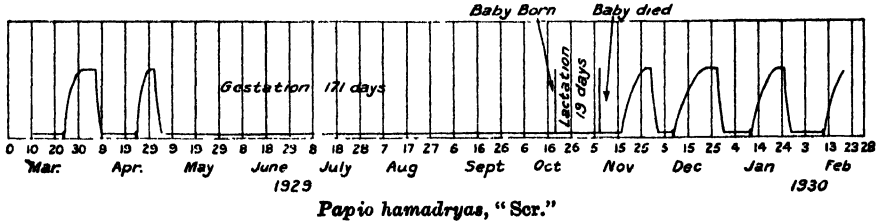
Papio hamadryas, "Ha.'

Chart 8.



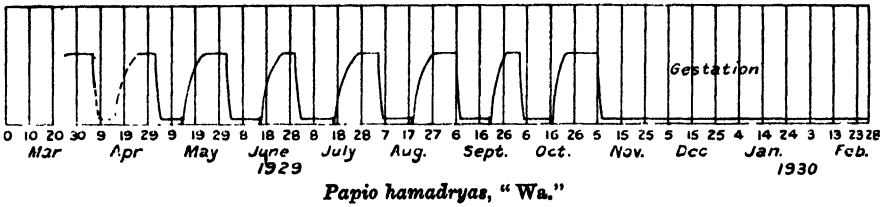
Papio hamadryas, "Sp."

Chart 9.



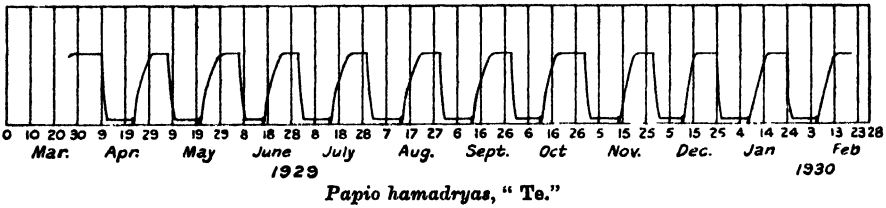
Papio hamadryas, "Scr."

Chart 10.



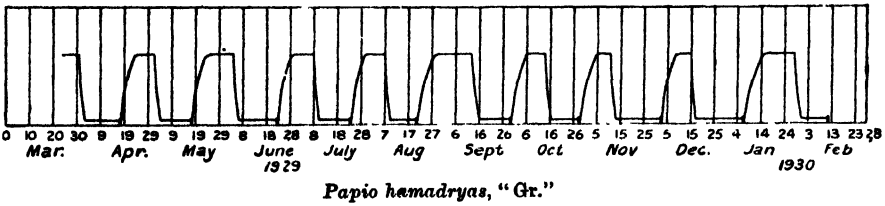
Papio hamadryas, "Wa."

Chart 11.



Papio hamadryas, "Te."

Chart 12.



Papio hamadryas, "Gr."

Charts 4 to 12.—Diagrammatic representations of the "menstrual histories" of nine Hamadryas Baboons, *Papio hamadryas*. **See Explanation of Charts, p. 754.**

The swelling is maintained, usually without any appreciable fluctuation in size, until about the middle of the cycle, when it suddenly disappears, the perinæum resuming its normal quiescent appearance. The regression of the swelling is usually heralded by peeling of its surface epithelium. Occasionally, however, peeling may become apparent earlier in the cycle. The onset of subsidence is sudden, and, generally, almost the entire swelling is absorbed within 24–48 hours. Frequently an animal which one morning shows its maximum swelling will on the next present almost a quiescent perinæum.

Apart from the changes in the perineal area, cyclical variation also occurs in the nipples, which become brighter in colour, and in the face, particularly around the eyelids. At the height of swelling the eyes are surrounded by a ring of red, brighter in the lower lid.

Vaginal secretion is more profuse while the swelling lasts.

The quiescent appearance of the perinæum varies from female to female. A certain residuum of swelling in the form of flabbly, thick folds is found in many. After the initial absorption of the swelling in the first 24–48 hours, the degree of prominence of the vulva and peri-anal tissues varies but little, if at all. The animal remains in this condition until the end of the cycle, when menstruation begins. Bleeding seems to be intermittent. As previously noted, the succeeding cycle begins with swelling of the perinæum, either during the flow or immediately after it.

An important point which requires detailed consideration, for reasons which will become obvious in the next section, is the exact time in relation to the cycle length when the pudendal swelling begins to be absorbed. I have already noted that it occurs about the middle of the cycle, and that it divides the cycle into a phase of swelling and a phase of quiescence.

In only two of twenty-three cycles where the limit of observational error was less than twenty-four hours did it occur at the exact middle of the cycle. In four the quiescent phase was of longer duration than the phase of swelling; in the first by 1 day, in the second by 4 days, in the third by 3, and in the fourth by 1, the average being 2·25 days. In the remaining seventeen cycles the phase of swelling was longer than the phase of quiescence by an average of 3·7 days, the range being from 1 to 8 days.

Considering the twenty-three cycles together, the phase of swelling was, on an average, of 2·3 days' longer duration than the phase of quiescence. The average is 1·7 days for 9 cycles of smaller duration than the average and probable modal cycle, 30; 2 days for 3 cycles of 30 days; and 3 days for 11 cycles of longer duration than the average cycle of 30 days. It is suggestive that the phase of swelling is relatively longer in longer cycles than in shorter ones.

In the twenty-three cycles under consideration absorption of the swelling commenced at some time within a period of six days, this period extending from two days before, to four days after, the middle point of the cycle.

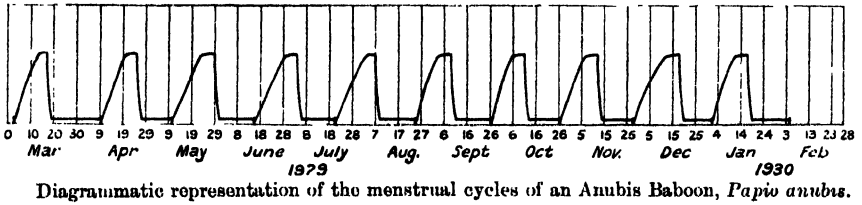
During 1929, observations were also made on the cycles of a young *P. hamadryas* female, who, judged by the stage of her dentition, is not fully adult. The date on which she first showed activity of her sexual skin is unknown. Bleeding occurred only four times during the year, in April, June, August, and September; this can be stated with certainty, for under the conditions of observation it would have been impossible to overlook its occurrence unless only a very small amount of blood was lost. Her perinæum is always in a state of hypertrophy, the clitoric and peri-anal swellings being continuously present. They undergo turgescence in regular monthly cycles, but never reach the size or turgidity seen in the adult female. Because of the small amount of difference between the quiescent and turgid appearances of the perinæum it is impossible to determine accurately the onset and decline of the swelling.

PAPIO ANUBIS.

A large fully adult female of this species has been under observation since the 1st of March, 1929. Up to the beginning of December 1929 eight cycles were noted (see Chart 13). The changes undergone are almost identical with those of the *Hamadryas* baboon, and the time relations of the phase of swelling and the phase of quiescence are approximately the same.

There are, however, certain small differences. The maximum perineal swelling reached is, relative to the size of the animal, less than occurs in *Papio hamadryas*. The appearance of the sexual skin at its maximum activity differs slightly from that of *P. hamadryas*, the peri-anal swelling being composed of a smaller, flattened, irregular hemisphere set upon a large one, while the entire swelling is not as furrowed as in some females of *P. hamadryas*. Another important difference is that the swelling, which begins either during or immediately after the catamenia, seems to increase gradually in size, reaching its maximum within a day of its absorption. Absorption is very rapid, being complete usually within 24 hours. During the quiescent interval there is no residuum of swelling, the labia majora and the peri-anal region reaching the level of the callosities.

Chart 13.



Diagrammatic representation of the menstrual cycles of an Anubis Baboon, *Papio anubis*.
See Explanation of Charts, p. 754.

The limit of observational error with this animal is less than 24 hours. Menstruation has been observed in each cycle.

The average length of the 8 cycles was 34 days, the range of variation being 30–38 days. In one of these eight the phase of quiescence was one day longer in duration than the phase of swelling. In one the two phases were equal. In the remaining six the phase of swelling was longer (on one occasion by three days) than the phase of quiescence. The average for the eight showed the phase of swelling to be one day longer than the phase of quiescence.

The onset of absorption of the swelling occurred at some time during a period extending from half a day before up to one and a half days after the mid-point of the cycle. In the majority of cycles absorption began after the mid-point.

PAPIO CYNOCEPHALUS.

A fully adult female of this species was under observation for the greater part of 1929. Up to the beginning of December seven cycles were observed (see Chart 14). The changes undergone are essentially the same as in *P. hamadryas* and *P. anubis*.

The maximum perineal swelling reached is relatively far greater than in either of the other two species; the peri-anal swelling is large and hemispherical, grooved and partially lobulated, with a transverse diameter of about 12 inches, a vertical diameter of 9 inches, and a depth of 9 inches. The clitoric lobe, about 6 inches by 3 inches, is smooth, and does not overlap its attached margins. The pubic lobe

and the area between the anus and vagina swell first, then the part dorsal to the anus, and finally the lateral portions The hypertrophy reaches its maximum within 7–10 days after the onset of the catamenia, swelling invariably beginning and proceeding during the flow of blood. Absorption is not as rapid as in *P. anubis*, and in this female there is always a residuum of swelling consisting of flabby folds of skin peri-anally and in the preputial sheath during the quiescent period.

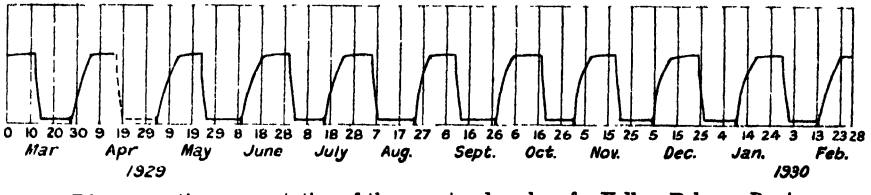
The margin of observational error with this animal is within 24 hours. Menstruation has been observed each cycle.

The seven cycles varied in length from 34–39 days, the average being 36 days. In every cycle the phase of swelling was of longer duration than the phase of quiescence, exceeding it by from one to six days, the average being three.

The onset of absorption of the swelling occurred at some time in a period from half a day to three days after the mid-point of the cycle.

In neither this female nor in the *Papio anubis* is there any suggestion, as there is in *P. hamadryas*, that the longer the duration of the cycle the longer relatively the phase of swelling.

Chart 14.



Diagrammatic representation of the menstrual cycles of a Yellow Baboon, *Papio cynocephalus*. See Explanation of Charts, p. 754.

Before dismissing the subject of the cycle in the normal adult, I may add that my observations agree with those of Gear in that the turgid perineal swelling of *Papio* is in no way sensitive, as Pocock suggests (1906). On the other hand, unless the manifestations of the cycle in *Papio porcarius* are totally different in South Africa (where Gear made his observations) from those in the same species in England (described by Pocock), Gear's observations on the time relations of the catamenia, the onset of swelling, and the absorption of swelling are inaccurate. There appears to be complete correspondence in the time relations of these three phenomena in all genera and species of monkey and ape which demonstrate external signs of a cycle.

The general plan of the primate cycle may be roughly summarised as follows. Menstruation occurs at fairly regular intervals of about 30 days. Immediately after the onset of menstruation, the sexual skin becomes active, reaching its maximum of activity before the middle of the cycle. Shortly after the middle of the cycle the sexual skin suddenly resumes its quiescent appearance, which it maintains until the onset of the next catamenia, when it again becomes active.

New World Monkeys.

Buffon, in his 'Natural History' (1775), remarks on the "periodical emanation" experienced by all Old World monkeys, and notes that this "emanation" does not occur in any New World primate. This observation is confirmed by

Geoffroy-Saint-Hilaire (Breschet, 1845). On the other hand, Rengger noted, in 1830, that females of the species *Cebus azaræ* occasionally exhibited a slight vaginal bleeding. The bleeding lasted two to four days, and, though not "periodic," recurred in three, six, or even ten weeks. This observation, however, has not been confirmed.

In my experience New World monkeys do not undergo menstrual cycles in captivity.

During the past year I have closely watched adult female squirrel-monkeys, *Saimiri sciurea*, adult female capuchins of various species, an adult female Black-faced Spider-Monkey, *Ateles ater*, and adult female marmosets, *Hapale jacchus*. In none have I seen any sign of cyclical bleeding or of cyclical variation in the conformaton of the external genital organs. It is possible, of course, that in captivity reproductive activity is usually in abeyance in this large group of primates. New World monkeys certainly show far less sexual behaviour than do Old World Monkeys.

In the London Zoological Gardens births amongst South American monkeys have been few and far between during the past 100 years. A White-throated Capuchin (*Cebus capucina*) in 1849, a Weeper Capuchin (*Cebus apella*) in 1885, and the Common Marmoset (*Hapale jacchus*) in 1832 and in 1892 complete the list. This does not include abortions, which probably have occurred from time to time, but which usually go unrecorded. One female marmoset, for instance, aborted twice during 1929.

So far as I know, the experience with South American primates in continental Zoological Gardens has been much the same.

Apart from the paper by Lucas, Hume, and Smith (1927), already mentioned, and the records left by Breschet (1845), I do not know of any record of either the sexual behaviour or the reproductive physiology of any New World monkey.

Pallas (quoted by Breschet) has left a record of vaginal bleeding in a marmoset. "A chaque époque du rut, la femelle avait un flux sanguin." On the other hand, vaginal bleeding has been observed on only one occasion in a Lister Institute marmoset *. Otherwise the experience at the Institute has been the same as mine, *i. e.*, in the marmoset there is no cyclical bleeeding or cyclical variation in the conformation of the perinæum apparent to gross observation.

Several births have taken place in the Lister Institute colony of marmosets. The animals are irradiated daily with a mercury-vapour quartz arc. Gestation lasts on an average 145 days, estimated from the last observed pairing previous to parturition (the range is 150–160 days), and lactation probably lasts 30 days. Attempts at coitus are repelled by the female during pregnancy †. "Oestrus" occurs and lasts for a short while only, the female at other times being disinclined for coitus and not "attractive" to the male. The nature of the attractive stimulus to the male has not been determined.

IV. The Physiology of the Sexual Skin.

Published records of investigations into the mechanism of the cycle in the sexual skin of monkeys and apes refer thus far only to *Macaca mulatta* (= *Macacus rhesus*).

In 1926 (*a*) Allen recorded the disappearance of external cyclical changes in the sexual skin of spayed females of the species *mulatta*. He also showed that the sexual skin of spayed females becomes active upon injection of follicular or

* I am indebted to Miss Hume for numerous data about marmosets kept at the Lister Institute, London.

† Geoffroy-Saint-Hilaire (Breschet 1845) reports an instance where a female marmoset copulated throughout pregnancy.

placental extracts (œstrin). Later in the same year (*b*) Allen noted that the sexual skins of two rhesus monkeys that had just ovulated (the one N on the 10th, the other E on the 14th day of the cycle) were "considerably reddened." Several other records are contained in his 1927 monograph. An animal (S) which was immature when observations were begun was "operated on the fifteenth day of her fifth cycle. At this time external colour was recorded as red I.," red I. indicating a mild degree of coloration. It was found that this animal had not ovulated in any of her five cycles. She was regarded by Allen as atypical. The sexual skin of a second female (LE) on the first day of the menses was light red in colour. A large corpus luteum was found in one ovary. No follicle larger than 1·4 mm. in greatest diameter was found in either ovary.

The ovaries of another female (2 E) which had not menstruated for three months previous to death were found to contain four very large follicles. "Extreme cutaneous reddening and swelling of the 'sexual skin' of this animal were noted at the time of killing."

One may correlate at this stage certain of Allen's findings. (*a*) "Ovulation often does not occur during many apparently normal menstrual cycles, and when it does occur, it probably happens between the tenth and the fourteenth day after the first appearance of the previous menses." (*b*) The sexual skin of spayed females may be activated with injections of the follicular hormone (œstrin). (*c*) The maximum activity of the sexual skin of normal healthy females occurs between the tenth and twentieth (see p. 703) days of the cycle, the colour fading before the approach of the catamenia.

These three facts taken in conjunction with one another suggest that the natural cyclical activity of the sexual skin of *Macaca mulatta* is the result of the stimulus of the follicular hormone which becomes operative at the beginning of a menstrual cycle, with the beginning of follicular growth, and which is removed * about the middle of the cycle (usually when the follicle ruptures). Activity of the sexual skin is thus part of the follicular phase of the menstrual cycle.

In his 1927 monograph Allen corroborated his earlier experiments upon the injection of follicular and placental extracts into spayed females. Here he showed conclusively that this experimental procedure is followed by signs of activity of the sexual skin. The more concentrated the extract used the more quickly does the sexual skin show signs of activity. After cessation of injections the sexual skin resumes its inactive appearance, though after two or three series of injections the colour fades only very slowly. The effects of the extracts upon the vaginal mucous membrane, the uterine mucous membrane, and the mammary glands will be discussed later.

In 1928 (*c*) Allen made several further contributions to our knowledge of the factor underlying activity of the sexual skin. A tubal ovum was recovered by operation from a female that had experienced amenorrhœa for 169 days. "During this interval the 'sexual skin' surrounding the external genital organs had been red and rough, the intensity of these phenomena undergoing five or six rather definite fluctuations, first fading and then coloring more deeply. Since these phenomena have been induced in ovariectomized animals by injected ovarian hormone, the deepening of the 'sexual skin' colour indicated increased ovarian secretion, probably dependent upon the growth of one or several follicles. At the time of the operation, the reddening was quite intense, although not at its maximum, and the skin in some regions was roughened and swollen and the hair standing on end. It is probable that the development of the follicle from which this ovum was extruded was concerned with the latest phases of coloring and swelling of the 'sexual skin'."

* But see Discussion at end of this paper.

In another paper (1928 *e*) he showed that injection of the follicular hormone, œstrin, into both normal and spayed immature rhesus macaques results in reddening and swelling of the sexual skin.

Hartman has shown that abnormally long persistence of activity of the sexual skin of *Macaca mulatta* is due to the presence of cystic follicles. In 1927 he published a brief account of a monkey that had menstruated on October 23rd, November 30th (1926), and January 10th (1927). By January 21st the sexual skin was highly coloured and swollen. "By February 7th the edema had attained tremendous proportions." She was operated on on February 11th. A large cystic follicle was found and was artifically ruptured. The sexual skin very soon resumed its quiescent appearance, and the animal menstruated 7 days later. This observation has been confirmed several times (Hartman, 1929 *b*).

Robertson (1929) has attempted to discover the effects induced in ovariectomized monkeys by injections of extracts of ovaries and implants of corpus luteum. The follicular hormone and the corpus luteum were given concurrently in the same series of experiments. Growth was induced in the uterus, but in none of his animals "had development of the uterine glands proceeded to a full premenstrual condition, as described by Corner for ovulating monkeys" (see p. 739).

Post-mortem examinations of female monkeys dying in the London Zoological Gardens have provided valuable data on the relation between the ovarian phase and the condition of the sexual skin.

An undersized female specimen of *M. mulatta* arrived in the Gardens on the 1st of December, 1929. She presented obvious signs of rickets and was otherwise in bad condition. Her stage of dentition corresponded to that of a girl about eight. Apart from permanent central and lateral incisors and first and second molars, her teeth were deciduous. When she arrived her sexual skin showed moderate signs of activity. Its colour gradually deepened and it commenced to swell, and by the 15th of December she presented an extraordinary degree of swelling. The pubic skin was thrown into thick rugous folds, the vulval lips and anus were swollen, and the skin of the dorsum of the base of the tail was in four thick folds. I have not seen as much swelling in any other female of this species. She remained in this condition until the 26th of the month, when she became acutely ill. She lay completely collapsed, her breathing was laboured, and she was unable to feed. As the usual measures failed to alleviate her condition, she was killed on the 1st of January, 1929. Her body weight was 2170 gms. It is interesting to compare the weight of this rickety undersized female with the weight of "somewhat over 3 kilograms," which Hartman (1928 *e*) considers to be the average weight of an adolescent female rhesus. During the month in the Gardens she was not seen to menstruate.

Autopsy showed her acute illness to be the result of pericarditis and bronchopneumonia. There was no sign of previous follicular rupture, but the right ovary contained one large follicle of 3 mm. diameter which appeared to be on the point of bursting. Several smaller follicles were visible in both ovaries. Whether she had ever ovulated is not as yet definitely known (the ovaries have not yet been examined histologically), but in the light of the work of Allen it is safe to infer that her exaggerated degree of sexual skin activity was related to the ripe follicle in her right ovary.

Several facts have been gathered regarding the correlation of the ovarian cycle and the activity of the sexual skin in *P. hamadryas*.

I noted previously (p. 711) that one adult female (C. 12) of this species was observed through only two cycles previous to her death. This female arrived at the Zoological Society's Gardens from Abyssinia on the 27th of June, 1927, and was then suckling a baby. I have been unable to find out when this baby was

weaned, but it was separated from its mother some months before observations were begun. The mother then occupied a cage by herself, and, according to her keepers, began to decline in health from the time of separation. When first examined, her sexual skin was about half the maximum size it could attain. The first observation, therefore, was made within a week after the commencement of the preceding menstruation, which had probably just ceased. Her subsequent history can be read in Chart 4. As indicated there, she died on the 19th of May, 1929, about twenty-four hours after the beginning of absorption of the swelling of the sexual skin. She had been rather ill and spiritless for several days before her death. The only pathological finding at autopsy was pulmonary congestion.

A very recent rupture of a follicle was found on the surface of the left ovary (see Pl. II.). An unsuccessful attempt was made to recover the ovum from the tube by flushing with warm Ringer's solution. The size of the ovary involved was $13 \times 10 \times 7$ mm. The area of the early corpus luteum, measuring to the limits of the yellow area seen on the surface of the ovary, was 8×5 mm. Near one pole of the somewhat oval area of the early corpus luteum was a brown depressed scar, the site of rupture. No plug projected through this rupture point. Numerous bright red vessels passed across the yellow area, the site of the rupture being surrounded by a vascular ring. The largest follicle visible on the surface was situated near the yellow corpus luteum area, and was 2 mm. in diameter. The right ovary did not contain any follicle as large. On its surface was a brownish scar about 2 mm. in length, probably the ovulation point of the previous cycle.

The microscopic appearance of this early corpus luteum, which was unfortunately sectioned through its base, is shown in Pl. II. In appearance it is similar to that described by Allen (1927) as typical of the early corpus luteum of *M. mulatta*. The section shows the rupture point on the surface of the ovary. There was no hæmorrhage into the central cavity, which, as in *M. mulatta*, is filled with a coagulum.

Another female of this species of baboon, kept at University College, London, by Dr. A. S. Parkes, died on the 29th of October, 1929, when her pudendal swelling was at its highest, fifteen days after the onset of menstrual bleeding. A mature follicle was found in the right ovary, while the left contained an old corpus luteum.

A second female, *P. hamadryas*, kept at University College, was operated on by Dr. A. S. Parkes, on the 29th of October, 1929, approximately on the thirty-eighth day of a cycle. It was impossible to ascertain the exact stage of the cycle, as the previous menstruation had not been observed. The calculation was made from the onset of swelling, which had persisted for seventeen days and had subsided twenty-one days previous to the operation, when the sexual skin was altogether quiescent. The right ovary, which contained a well-developed corpus luteum, was removed. She was operated on a second time on the 29th of January, 1930, seventy-two days later, by Mr. L. Williams, F.R.C.S., of University College Hospital, London. No vaginal bleeding was observed during this interval; she had, however, shown two cycles of pudendal swelling, and the second operation was performed two days after the beginning of the third cycle, when her sexual skin was about one-third the maximum size it could attain. At this operation the remaining ovary and the rest of the uterus were removed. The ovary contained a medium sized follicle (3 mm.), not projecting from the surface of the ovary. Twenty-four hours after the operation her pudendal swelling had diminished almost by half. Seventy-two hours later it was less than the usual residuum of swelling normally shown by this female in the quiescent phase of the cycle.

Although experimental proof that the pudendal swelling of *Papio* is due to the follicular hormone is lacking, one may safely infer it from consideration of the above data. Accurate data regarding the size of follicles to be found in the ovaries of menstruating baboons, or in fact of any primate, are unfortunately lacking. It would seem, however, that the condition of the baboon sexual skin at any point in a cycle is a reflection of the phase in the ovary at that particular time. Any cycle ends with menstruation. The onset of destruction of the endometrium at menstruation is, in cycles with ovulation, a sign of the removal of the stimulus of the luteal hormones (see p. 748). The luteal secretions have been shown to be responsible in many lower mammals for the suppression and postponement of œstrus. "The presence of a corpus luteum in one ovary is sufficient to inhibit the œstrus-producing activity of both ovaries"—*i.e.* the production of œstrin (the follicular hormone) (Parkes, 1929). Where œstrus has been artificially inhibited by the injection of luteal extracts, follicles after a moderate degree of development undergo atresia (Papanicolau, 1926). One may assume that at the normal termination of a luteal phase at menstruation, the follicle which will proceed to ovulation in the ensuing cycle (provided ovulation occurs in that cycle) is then about medium size and commences to develop rapidly. This assumption is supported by the fact that swelling of the pudendal area in the baboon generally begins during menstruation; this swelling is due to the hormone œstrin which is found in the follicle, as well as in other places. As the follicle matures the effects of the hormone become more intense. The swelling in the Anubis baboon, for instance (p. 715), seems to reach its maximum just the day before its absorption. Absorption of the swelling is sudden and rapid in the baboon, and appears to coincide with ovulation, which therefore usually occurs slightly later than the middle of the cycle. Rupture of the follicle, as in the lower mammal, indicates the apparent termination of the follicular phase, that is, the point of cessation of obvious activity of the follicular hormone œstrin.

During the interval between ovulation and menstruation in the non-pregnant baboon, *i.e.* during the luteal phase, the sexual skin is inactive. During pregnancy and lactation—the fullest expressions of the luteal phase—the sexual skin is also inactive. This latter point will be referred to again in a later section.

In the lower mammal, *e.g.* the ferret, œstrin is responsible for œstrous changes in the accessory organs. The swelling of the sexual skin of the baboon is thus analogous to the œstrous swelling of the ferret vulva.

The series of changes in the sexual skin of *M. mulatta* are strictly comparable with those of *Papio*. In *Macaca mulatta*, however, the prominent change is one of colour, and without an adequate objective standard it is impossible to describe the varying intensities of red exhibited by the sexual skin of the adult female. It is for this reason more than any other, as I have already remarked, that accounts of the sexual skin phenomenon in *M. mulatta* are vague and frequently conflicting. Collings found that the maximum of coloration in *M. mulatta* was reached during the third week of the cycle, while Allen noted that coloration was most marked during the tenth and twentieth days of the cycle. So far as is known, ovulation in *M. mulatta* occurs between the tenth and fifteenth days of the cycle (Allen 1927, Hartman 1929*f*). If full value is to be attached to the statements of Collings and Allen on the late limit of sexual skin activity in *M. mulatta*, it would seem therefore that activity continues after the removal of the œstrin stimulus at ovulation. It is more likely, however, that the variation which they describe is due to the difficulty of defining limits to the activity of the sexual skin because of the absence of estimable swelling. In the baboon the colour of the sexual skin changes but little compared to its variation in prominence; the colour of the quiescent perinæum is little different from that of the

swollen perinæum. Indeed, without the variation in size it would be difficult to describe the cycle in the baboon sexual skin.

As previously noted, it usually takes from 24–48 hours for the absorption of the swelling in the baboon. It is possible, therefore, that a similar time elapses in *M. mulatta* before signs of the activity of the follicular hormone disappear. On this point there are data. The swelling and colour of the sexual skin of the macaque with a cystic follicle ruptured artificially by Hartman "were greatly reduced" after three days. After six the sexual skin was completely quiescent. It is unfortunate that there is no record of the condition of the sexual skin the day after the operation. Allen (1927) notes that by the middle to the end of the second week following ovariectomy performed on rhesus macaques showing a maximum of swelling and coloration, the sexual skin becomes completely quiescent. This observation too is, unfortunately, rather vague. His data on the effects of œstrin on spayed females are, however, more detailed. His method was to inject preparations of the follicular hormone daily for a certain number of days, varying the amount given at set periods in the series of injections. In one series of 20 injections the maximum dose was given on the sixteenth day. The maximum effect on the sexual skin was attained on the eighteenth day, the colour then fading "rapidly to pale red on the third day after the last injection or the seventh day after the maximum dose." In another series of nine injections on the same female where the maximum doses were given on the eighth and ninth days, "'the sexual skin' became considerably roughened and swollen toward the end of this series. The color had faded to very light on the fourth day after the last injection, and had completely disappeared by the eleventh day." These and similar experiments of Allen's have shown conclusively that a decrease in the amount of hormone injected, or cessation of injections, is followed within a day or two by a decrease in the signs of activity of the sexual skin. From his protocols (1927) one may infer, too, that coloration and swelling of the sexual skin vary independently of each other. In one series of injections into a spayed female, colour persisted in the sexual skin for eighteen days after the last injection of the series. Whereas "an extreme degree of swelling or pouching" which had accompanied the maximum colour had "completely disappeared by the fourth day after the last injection." This, too, is a fairly common experience in normal females. One frequently notes a relatively sudden disappearance of the swelling of the sexual skin in rhesus macaques (see quotation from Corner, p. 703). This point will be referred to again in the discussion on pregnancy in Section VIII., p. 737.

From Allen's experiments, and from consideration of the somewhat abrupt disappearance of swelling in the baboon, it would seem that the maintenance of sexual skin swelling depends upon the continued secretion of œstrin. The amount secreted probably increases from the beginning of the cycle and reaches a constant about the middle of the preovulation stage of the cycle. Judging by Allen's experiments, there seems to be a slightly cumulative action of the hormone. The amount of activity of the sexual skin at any time, however, depends mainly upon the amount of œstrin being secreted or injected at that time. One may infer, therefore, that at the beginning of swelling less œstrin is being secreted than at the time of maximum swelling. The period which elapses before the disappearance of signs of activity after the cessation of injections in the experimental animal is slightly longer than the similar period which normally follows in the baboon after ovulation. This may be due to the fact that in the normal animal ovulation is immediately followed by development of the corpus luteum.

There can be no doubt that the physiology of the sexual skin is the same in

M. mulatta as in *Papio hamadryas*. One may safely infer from the similarity in time relations of the sexual skin phenomenon in other primates that œstrin is the responsible factor for the swelling and coloration of the sexual skin of all monkeys and apes.

V. Nature and Changes of the Sexual Skin.

(a) *General.*

According to Collings (1926) excitement frequently causes "a marked but temporary fading of the color" of the sexual skin in *M. mulatta*. "A like effect was obtained by suspending the monkeys by the hind legs for a short time. Digital pressure over the part caused a local blanching at the point of pressure which would last for two or three seconds and which appeared to color up from the periphery of the pressed area towards the center. The application of chemical irritants and of cold by ice-packs gave rise to an even more marked reddening. The phenomenon as a whole was more marked during warm sunny weather than during cold or damp weather. Furthermore, it might be added that blood welled up much more profusely from all incisions made in this area than from skin incisions made in other regions."

It may be remembered that colour changes also occur in the nipples and face. These, in certain monkeys, show cyclical changes corresponding to those in the sexual skin area. Unlike Collings, I have not noted any effect of excitement on the sexual skin. My observations go to show, however, that the colour of a monkey's face remains the same or may deepen in excitement.

(b) *The Colour of the Male.*

The hindquarters and face of the male hamadryas baboon are coloured pink to bright red, the hue varying in different animals. Momentary and fairly long sustained variations in intensity of colour occur; excitement, for instance such as is caused by fighting, frequently intensifies the colour.

The facial and perineal colour of male rhesus monkeys also varies from individual to individual and in the same individual from time to time. I have also noted marked variations in the facial and perineal colour of a male Japanese macaque, *M. fuscatus*.

Hartman (1928 *e*) notes that male rhesus monkeys "also exhibit brilliant reddening of the buttocks, which changes from time to time, probably according to the general state of well being of the individual."

Allen (1928 *b*) noted the sudden appearance of reddening in the sexual skin area of a large seven-year old male *M. mulatta*. He remarks that it has been reported that male rhesus monkeys normally show this reddening during the breeding season. (Darwin (1871) also made this observation.) Allen inferred that the causative factor of coloration in the male might be the male sex hormone. Experiment showed that injection of the testicular hormone of this particular monkey in the form of ground testis and epididymis produced not "the slightest indication of even a partial œstrous reaction" in ten ovariectomized rats. Apart from this experiment, the coloration of the male has not been investigated. Injection of both œstrin and testicular hormone into castrated adult males suggests itself as a possible means of discovering more about the male sexual skin.

(c) *The Innervation of the Sexual Skin.*

Langley and Sherrington (1890–1892) have shown that the sexual skin of the rhesus macaque is supplied by the sensory roots of the same nerves whose motor

roots supply the vagina, *i.e.* the first, second, and third sacral. The pilo-motor nerves to the hair of the sexual skin pass through the lumbar sympathetic trunk from the 12th thoracic, 1st, 2nd, and 3rd lumbar nerves. The erection of these hairs persists long after the cessation of experimental stimulation of the lumbar sympathetic cord.

Histology.

Collings (1926) has made a close study of the histology of the sexual skin of *M. mulatta*. His results may be briefly summarised. The skin is thicker over the buttocks than over other parts of the body. The tissues under the sexual skin are of looser mesh than in other parts of the body, elastic fibres are more abundant, and hair follicles, sebaceous and sweat glands are larger. The deeper vessels in the subcutaneous layer are larger than normal in the active sexual skin. The papillary layer of the sexual skin has a rich blood-supply. A rich vascular plexus is situated immediately beneath the epithelium, the vessels being thin-walled blood-channels frequently larger than the feeding arterioles in the subcutaneous tissues. Collings found "a direct correlation between the degree of reddening, the size of the superficial vessels, and the degree of engorgement. In the reddest specimen were found the largest of the superficial thin-walled blood-channels, and in these specimens the engorgement was most marked."

The histology of the pudendal swelling of the baboon does not appear to have been investigated as yet. There is very little bleeding when the swelling is incised. On section it is white and rather like a coagulum. In some parts the incised œdematous swelling is purplish in colour.

The swelling in the baboon seems to be mainly due to a transudation of fluid into the intercellular spaces. It is impossible as yet to say how this transudation is effected. The hormone œstrin is, no doubt, contained in the blood circulating in the vessels of the pudendal area. In the rhesus macaque it causes dilatation of the minute thin-walled vessels beneath the epidermis, though only a small amount of transudation occurs in this species. In the baboon, however, transudation is considerable. The following are a few of the immediate questions which are suggested from these considerations. (*a*) Does the hormone act directly upon the capillary walls, causing dilatation? This problem could be approached by the usual experimental methods. It would be necessary first to investigate the possibility of nervous control of the vessels of the sexual skin area by means of section of the nerves involved. Another method of approach to a solution of the problem would be the investigation of the effects of œstrin and control fluids upon isolated portions of quiescent baboon sexual skin and skin from other parts of the body, kept in a suitable medium. (*b*) What is peculiar to the capillaries of the sexual skin that they alone dilate, leading to transudation, while capillaries in other parts of the body are on the whole unaffected? This question suggests a study of the histological differences between the skin of different parts of the body. It might also be possible to discover why the lower eyelids of some hamadryas baboons become more deeply coloured than other parts of the face during the follicular phase of the cycle. (*c*) What is the cause of the transudation? Why should transudation occur in one species and not in another? Does transudation depend upon the amount of circulating œstrin, and, if so, would it be possible with excessive dosage to produce a degree of swelling in the sexual skin of a spayed rhesus macaque which would parallel that seen in species which normally show marked swelling of the sexual skin?

Another problem is suggested by Langley and Sherrington's observation that erection of the hairs of the sexual skin is caused by stimulation of the lumbar sympathetic cord; for during the phase of coloration in the rhesus macaque these

hairs are erect. While it is possible that the erection of hairs is the result of direct stimulation of the pilo-motor nerves through local pressure rising out of the engorgement of the sexual skin area, it is conceivable that there is a nerve-hormone relationship.

VI. The Biological Significance of the Sexual Skin.

Various interpretations have been made of the phenomenon of the cyclical change in the sexual skin. Von Fischer (1876) suggested that the colour of the hinder parts of the female monkey renders her conspicuous to the male when viewed from afar. Darwin (1876) criticised this suggestion, giving as his opinion that, "as monkeys are such gregarious animals," he would have thought "that there was no need for the sexes to recognize each other at a distance." He continues, "it seems to me more probable that the bright colours serve as a sexual ornament and attraction." Darwin did not differentiate between the cyclical coloration of the sexual skin of the female macaque and the bright coloration of the face and hindquarters of the mandrill. In his argument for sexual selection as a factor in evolution, both were considered to be ornamental characters, even though he admitted that the rhesus monkey was the only mammal he knew in which the female was more ornamental than the male. The coloured hinder parts of monkeys were grouped with their beautiful and varied coat colours as characters "acquired through sexual selection exclusively as ornaments." In Darwin's opinion, as "monkeys have the habit of turning their hinder ends towards other monkeys, it ceases to be at all surprising that it should have been this part of their bodies which has been more or less decorated."

These views of Darwin's are interesting. They are, however, rather unsound, for, apart from their anthropomorphic point of view, they are based on incomplete and uncontrolled observations. In any case, the classification of the cyclical phenomenon, which we now know to be due to the action of the hormone œstrin, with permanent secondary sexual characters, which are almost certainly not caused by that hormone, is quite unjustifiable.

Pocock (1906) went back to Von Fischer's view, considering that the swelling and reddening "serve as a source of information to the males" of the sex and condition of the female when seen at a distance. This suggestion again assumes that the sexes are normally segregated, which, as Darwin pointed out, is incorrect. Pocock also lends his support to Darwin's view that the coloration is an ornamental character. "It may be that the colour and inflammation appeal to the æsthetic sense and sexual emotions of the males and act as an aphrodisiac impelling them to pair with females in which the characters are pronounced rather than with those in which they are poorly developed or absent."

Two important aspects of the problem must be made clear. (*a*) Monkeys have colour-vision. Any doubt which might have been cast by the work of Waston (1909), amongst others, upon the colour sense of monkeys has been dispelled by the work of de Haan (1925), Köhler (1927), and Kohts (see Yerkes, 1929). This is important, for it has frequently been said that monkeys do not see colours. If this were true, the reddening of the macaque sexual skin, for instance, could have no biological significance. (*b*) No segregation of the sexes takes place in primates. The sexes are permanently together. Moreover, monkeys are not promiscuous. The literature provides sufficient evidence to enable one to make the generalization that the tendency of sub-human male primates is towards polygyny. Every adult male attempts to secure for himself as many females as possible. There is no selection. The most dominant males secure for themselves the largest number of wives, and maintain ownership until they are deposed. In the colony of fifty hamadryas

baboons owned by the Zoological Society of London, where adult males outnumber adult females by six to one, daily observations throughout the year 1929 failed to show more than three instances of a female having sexual relations with any male other than her "husband." These occurred when the "husband's" back was turned (see Zuckerman, 1929).

It is generally believed that sub-human primates mate at all times, and that they experience nothing similar to the œstrus of the lower mammal. According to Corner (1923 *b*) "the manifestations of sexual desire may be considered to be diffused over the entire reproductive cycle." This, too, is Allen's opinion (1927), while Hartman writes (1928 *e*) that "as a general rule, the females (*rhesus macaques*) will accept the male whenever given the opportunity. We have at least a hundred observations on this point. Some females have, however, consistently refused the male, and certain ones have an antagonism to one or the other of our males, but the stage of the menstrual cycle has nothing to do with their refusal or acceptance." In another paper (1928 *d*) he makes the generalization that "primates have no definite 'heat' periods, but copulate at any time, some species with great frequency."

Miller (1928) made a close study of the very limited literature on this subject and was led to believe that both sexes of sub-human primates "are ready for sexual activity at all times"*. Hamilton's paper on "Sexual Tendencies in Monkeys and Baboons" (1914) was consulted, and from it Miller inferred that female sub-human primates "were not subject to a psychological œstrous cycle, but were ready to accept the male at all times when not physically incapacitated (as by traumatism or recent parturition). The males, far from having their sexual responses solely and automatically released by the female when in one definite and special physiological condition, or having their sexual interests fall into abeyance outside of a season of rut, were sexually attracted by any adolescent or adult female at any time." All this, however, is pure inference from negative data. Hamilton's paper contains not a single reference to œstrus or rut, and menstruation is mentioned only as a sign of sexual maturity. Miller's conclusions, if they are to be considered sound, must have a firmer foundation than this. Other sources consulted were Montané's papers on the birth of a chimpanzee in Cuba (1915, 1928). According to Montané, the chimpanzee copulates at any time, including pregnancy. Kempf (1917) is also quoted. His paper concerns the sexual activities of six rhesus macaques, only one of which was a female. The observations are mostly on homosexuality. The paper contains no definite reference to œstrus in the female or to rut or periods of increased desire in the males. This, however, is but negative evidence in favour of Miller's view. Kempf's paper contains one or two gross inaccuracies. For instance, the female rhesus described is said to have been six months old, but she is described in one place as menstruating (see p. 703).

Miller also refers to Sokolowsky's statements (1923) regarding a chimpanzee. Sokolowsky writes that a certain adult male chimpanzee "demanded repeated intercourse every day with his females. For this purpose he sprang down and seized one of the females who even if she struggled at first, had to yield finally to his superior strength." This is hardly justification for Miller's inference that "no periodical œstrus was apparent."

In addition to Hartman's statement, which I have already quoted, and two others which do not in any way add to his argument, Miller also quotes two statements which are definitely against his conclusions. The first is Köhler's statement regarding the chimpanzee (1927). This I have quoted in full on p. 698. Miller does not quote as fully as I have done, and omits reference to the access of sexual desire which, in the female chimpanzee, accompanies pudendal enlargement,

* This study was made in order to refute Malinowski (1927), who had stated that apes experience a period of heat.

noting only the quiescence of desire during the catamenia. His quotation has, therefore, little point. The second is from Gear's paper, "The Œstrous Cycle of the Baboon" (1926). This Miller admits to be the only record he found that points "to the occurrence of a period of rut in any primate." Gear writes that "during the period of the genital enlargement a marked change in behaviour occurs. The animals lose their restlessness and usually remain quiet in a corner of the cage, even ceasing to care for their fur. . . . In the females under observation, it was at this time that they permitted and even solicited the advances of the male, resulting in frequent acts of coitus."

It is on such slender evidence, then, that Miller arrives at the conclusion that sub-human primates are equally ready for sexual activity at all times.

Before mentioning my own observations bearing on this problem, other statements conflicting with Miller's view may be mentioned.

Geoffroy-Saint-Hilaire (Breschet, 1845) wrote that "les femelles qui reçoivent fréquemment les mâles en tout temps, deviennent, quand a lieu cette turgescence extrême des parties sexuelles, très-avides de l'approche de ceux-ci. Le rut est surtout très-ardent vers le commencement et la fin de l'écoulement." This statement, while it associates the follicular phase swelling with most marked sexual behaviour, is incorrect with regard to the relationship between swelling and menstruation (see also p. 697). Geoffroy-Saint-Hilaire also noted that coitus was infrequent during pregnancy, when the cycle was suppressed.

In their paper on the Marmoset (1927), Lucas, Hume, and Smith note that the mating periods of the marmoset seem to be demarcated. They write, with reference to a particular female, that coitus was observed on March 23rd and during the next two or three days. "Then attempts became fewer and less accceptable to the female, and finally ceased altogether. During the ensuing months there was no sign of œstrum, and when the young male was at liberty he paid no more attention to the female, through the bars of the cage, than he did to the other male." Accurate data about mating in the non-pregnant marmoset are lacking, but both the Lister Institute records and my own observations at the London Zoological Gardens suggest that the female normally desires and tolerates mating only at set times.

Pocock (1906) described the pairing of baboons as occurring after the catamenia, *i. e.* during the period of pudendal enlargment, and correlates the swelling in the female with "the extreme length of the intromittent organ in the male of Baboons." He does not state whether pairing also occurs during the quiescent period of the cycle.

Fox (1929) describes a period of heightened desire in the female chimpanzee, and writes regarding a pair living in the Philadelphia Zoological Gardens that the sexual act is more frequent, more desired by the male, and more acceptable to the female during the period of perineal swelling. On the other hand, a pair of orangs in the same animal collection perform the act daily without relation to the menstrual cycle.

According to Dr. C. Dobell, the rhesus monkey mentioned on p. 703 becomes very uncertain-tempered and quarrelsome at the time of reddening (but not at menstruation). She then is sullen and disobedient, and continually gnashes her teeth.

I have had the opportunity of observing many species of monkey, and my conclusions about their behaviour are based on continuous observation at the London Zoological Gardens over a period of fully eighteen months. Both negative and positive facts are recorded here.

An adult female Siamang and an adult male Hoolock Gibbon share the same cage. They have been together almost four years, and both are extremely active and in excellent condition. They have never been seen to mate or to behave in a manner which could be construed as sexual (see p. 699). An adult Silvery Gibbon,

Hylobates lar (see p. 699), has been observed thus far over a period of 2 months. She is tame and usually approaches the bars of her cage to be stroked. No cyclical variation in the intensity of this social gesture of hers has been noted.

An adult male Entellus Langur shared a cage with a Grey-cheeked Mangabey for over a year. This is the mangabey described on p. 701. Her behaviour during the periods of pudendal enlargement has almost continuous sexual reference (see below). During these periods she would approach the male, hindquarters first. There was never any response on his part *. This is similar to the experience recorded by Heape (1894), who kept adult male Entellus Langurs in cages with adult females of the same species in the hope that they would mate. "Many of the females seemed quite prepared for copulation, and tried to induce the male to fertilize them, but without success."

There are several cages in the Monkey House of the London Zoological Gardens occupied by adults of both sexes of many species of the genus *Cercopithecus*. While certain of the males of this genus are obviously potent, neither I nor keepers in the house recollect ever having observed their mating with the females. At the same time mating does occasionally happen, for species of this genus have on rare occasions bred. Compared, however, with many others, this group of monkeys show little sexual activity.

My observations on mangabeys are limited to one immature female and the Grey-cheeked Mangabey previously mentioned. The immature monkey has not yet been seen to behave in any obviously sexual manner.

The other becomes exceedingly sexual during her periods of pudendal enlargement. She is at present alone in her cage (see above). During the stage of perineal quiescence, that is, in the latter half of the menstrual cycle, she is variously occupied, jumping about wildly, clattering her feeding-tin, attracting visitors, fighting and threatening her neighbours. During this stage she rarely examines her genitalia. When she clambers up the wire to be stroked, she is content with having her arms and chest played with. But in the stage of pudendal enlargement her attitude changes completely. She continually examines her swollen perinæum, rubs it on available surfaces, and presents herself, buttocks first, to visitors (this form of behaviour will in future be referred to as "presenting"). If attempts are made to stroke her during this stage, she usually tries to bring her pudendum into contact with one's fingers. At the height of swelling her sexual excitement becomes intense. Its abatement is as dramatic as is the subsidence of swelling.

In the Lister Institute mangabey mentioned on p. 700 the desire to mate was strongest at the height of swelling.

Several species of macaque have been observed.

Three adult female bonnet monkeys (*Macaca radiata*) share a cage. On rare occasions homosexual behaviour has been noted; it was impossible to correlate these with the stage of the cycle (see p. 705). There are several adult female Kra monkeys, or common macaques (*Macaca irus*) in the collection. Mating has been observed on very rare occasions.

While my observations on the rhesus macaque (*Macaca mulatta*) agree broadly with what is usually recorded, *i. e.* that rhesus macaques copulate at all times, they also extend beyond this generalisation. Many rhesus macaques live in, and pass through, the London Zoological Gardens, but to judge from published records, they are far less occupied sexually than are members of the same species kept in captivity in the United States of America. I am convinced that the mating of rhesus macaques in the London Gardens is more frequent when the sexual skin is active. The female then welcomes and even solicits the male's advances, and the males are more attracted by the females.

* Breeding between different species of monkey has frequently been recorded. Mating between different species occurs under captive conditions in mixed cages almost as freely as mating between members of the same species.

There are at present living in one particular cage six rhesus monkeys. The leader is a large adult male. He is particularly attached to an adult female, whose companion he has been for two years. The other four members are recent occupants of the cage. This group was led by an adult male who is now completely suppressed by the older pair and is of lowest "caste" in the group of six. The second dominant member of this group was an adult female. She, too, is now a completely dominated monkey. The other two are an adolescent male and an adolescent female who have attracted little of the attention of the original two inhabitants of the cage and are correspondingly but little suppressed. Apart from the sex play of the adolescents, sexual behaviour is manifested by the male leader and by the two adult females. This male copulates with both females, paying attention to the suppressed female only when her sexual coloration is at its height. At other times he is either oblivious of her presence, or becomes her tormentor. He mates with his own female rarely in her quiescent state and relatively frequently when her sex skin is active. On such occasions they sometimes copulate repeatedly in an interval of an hour.

A pair of adult Japanese Monkeys (*Macaca fuscata*) share a cage. Over a period of more than a year neither I nor the keepers have observed any behaviour of sexual significance.

Two adult Pig-tailed Monkeys (*Macaca nemestrina*) have been together, except when the male was separated during the weaning of their child, for two years. They are in excellent condition. Copulation is observed several times daily irrespective of the stage of perineal swelling. Their excitement is, however, definitely greater during the stage of maximum perineal enlargement. The same pair copulated freely during the female's pregnancy, throughout which her perinæum was quiescent. They also copulated immediately (within six hours) after parturition.

The sexual activity of a female baboon varies directly with the amount of pudendal swelling she exhibits. The "attractiveness" of a female baboon to a male also varies directly with the amount of her pudendal swelling. These two statements are borne out by observations on isolated female baboons and on females in normal social relationship with male baboons.

During the quiescence of the perineal area, caged baboons in the London Zoological Gardens very rarely, if at all, exhibit sexual interest. When coaxed to the wire of the cage they do occasionally "present," but more frequently their interest lies in having their fur "picked." "Presenting" is not always an immediate sign of sexual desire. It may, on occasion, be a friendly greeting, but it is frequently a sign of submission. It is exhibited as a reaction by males as well as females. Its ultimate significance is, however, sexual, and it is prompted most frequently and most insistently by sexual desire. During the phase of pudendal enlargement female baboons are more easily coaxed to the wire of their cages than in the quiescent phase, "presenting" insistently without encouragement. A keeper whom I asked to obtain for me vaginal smears of two baboons in order to study the vaginal cycle (see p. 741) had no difficulty during the earlier half of the cycle, but usually found it impossible to obtain smears after the swelling had subsided. Even if he managed to coax them to the wire and they presented, they would not allow the passage of a spatula.

On "Monkey Hill," where a colony of hamadryas baboons of both sexes and all ages lives, it is possible to observe the behaviour manifestations of the sexual skin cycle under relatively "natural" conditions. The bond between a male and his female is closest when there is greatest pudendal swelling. Elsewhere I have stated that at such times the female hardly ever moves from the male's side, whereas in the quiescent phase she may sit several feet away

from him (1929). Copulation is most frequent during the stage of perineal enlargement, though it also occurs during the quiescent phase. When more than one female is owned by a male, priority in the harem is taken by the female "in œstrus". Under such circumstances the male overlord copulates almost entirely with the female who is in the phase of pudendal enlargement. I have never observed the male mating at such a time with a second female of the harem who is in the quiescent phase. The quiescent female of a harem is more active than the female with pudendal enlargement, spending the day at some distance from her male; the "œstrous" female spends the day sitting and moving in close contact with her overlord. The instances of "infidelity" which I have noted (p. 726) have involved only the quiescent female, never the "œstrous" female.

I have not noticed the temperamental change in the "œstrous" female described by Gear (p. 727) in caged baboons. It is, however, a very obvious occurrence on "Monkey Hill."

The first generalization which one may make from these records is that primates which show marked cyclical changes in the sexual skin are more active sexually than those that do not. Environmental conditions can hardly be considered a responsible factor for this difference in behaviour. All the monkeys in the London Gardens (except those on "Monkey Hill") are housed and fed in the same way, and this present environment cannot be said to approach the natural conditions of any one species more than any other. Many species show greater adaptability to captive conditions than do others. This may have important bearing upon reproduction and sexual activity, but at present it is a factor difficult to gauge. The only obvious correlation is between sexual activity and activity of the sexual skin.

The mechanism of this correlation is suggested by Langley and Sherrington's observation that the sexual skin (of the rhesus macaque) is supplied by the sensory roots of the same nerves whose motor roots supply the vagina. When the sexual skin is swollen with œdema its sensory nerve endings are stimulated by pressure. Apart from this obvious means by which the animal's attention is directed upon its genital organs, there doubtless occurs reflex excitation of the motor nerves of the vagina, leading to its increased tonicity and possibly also to movement of its muscular walls.

The biological significance of sexual skin activity is therefore obvious. Mating occurs most frequently when swelling and coloration are at their height, *i. e.* when the follicular hormone œstrin is most active, just before ovulation. In this way œstrin serves the same purpose in primates that it does in the lower mammal. With few exceptions * the lower mammalian female will mate only when she is in "œstrus", which is a psychological state reflecting a series of physiological changes, the direct cause of which is œstrin. Œstrus synchronises with or follows soon after ovulation. The effect of œstrin may therefore be said to be the prevention of sterile mating. This is also what probably would occur with sub-human primates, under normal conditions—that is, when male monkeys need not necessarily apply themselves to only one female. The female gradually passes into an attractive condition, and remains in that state while she becomes desirous. After ovulation she reverts into her unattractive and non-desirous state. In this way mating chiefly takes place when it is likely to be fruitful and rarely occurs when it might interfere with and prevent implantation.

Even under completely normal conditions, however, the matings of monkeys are not altogether controlled physiologically. The fact that monkeys mate outside the phase which corresponds to the œstrus of the lower mammal is partly due to the conditioning of their behaviour that results from the possession of a highly

* Perhaps only the rabbit, when in an artificial environment (Hammond, 1925).

efficient sensori-motor apparatus. For apart from the desire for sexual satisfaction, female monkeys are known to offer themselves sexually in order to obtain access to an enemy, in order to escape from an enemy, and for several other similar reasons (Hamilton 1914, Hofschläger 1925, Zuckerman 1929). Mating, however, is far less determined by psychological than it is by physiological factors.

VII. Puberty.

In the lower mammal the first definite sign of puberty is the first œstrus. Apart from subjective symptoms, the first definite sign of puberty in women is the first menstrual flow. In monkeys the first sign of puberty is activity of the sexual skin, corresponding to the first œstrus of the lower mammal. Thus the first effects of sexual maturity in both monkey and lower mammal are due to the follicular hormone œstrin.

Little is known of puberty in the gorilla. Congo, the young female investigated by Yerkes, was approximately 6–7 years old when she died. She then weighed about 160 pounds, and "each jaw carried two pairs of incisors, one pair of canines, and four pairs of molars" (1928). One may tentatively infer from this description that the incisors were permanent, and that the third and fourth molars in each jaw were also permanent, the first and second probably being milk molars. This female had not menstruated. Yerkes, however, believes that she died just before puberty. The chimpanzee is said to reach maturity between the ages of 8 and 12. Yerkes (1929), after critical examination of all available information, came to the conclusion that "the chimpanzee matures sexually slightly more rapidly than does man in the tropics." The gibbon is said to become sexually mature when seven years old (see p. 698).

The female orang, too, is believed to become sexually mature when about eight years old.

The only published records of puberty in other sub-human primates refer to *M. mulatta*. Allen (1927) mentions reddening and swelling of the sexual skin as the main sign of the onset of sexual maturity in this species. He points out, moreover, that the first menstruation is not necessarily a sign of ovulation, as menstruation may occur without ovulation. He has also recorded the weights of three monkeys when they first showed these signs of sexual skin activity and when they first menstruated :—

	Sexual skin.	Menst.
N.....	3·51 kgms.	4·47 kgms.
S	3·13 kgms.	3·13 kgms.
B.....	2·9 kgms.	3·17 kgms.

"The first menses in animals S and B followed in 6 to 10 days after the first appearance of reddening, while in N the first menstrual bleeding was delayed until more than 50 days after reddening first appeared."

Hartman's views on puberty in the rhesus macaque have been noted on p. 703 and p. 719. There is no record in his papers of the interval which elapses between the first appearance of sexual skin coloration and the first menses.

The history of a female rhesus which died in the London Zoological Gardens about the time of her puberty is recorded on p. 719. She had probably never ovulated, and during the month in the Gardens did not menstruate. Her sexual skin had been active for over a month, and at autopsy a 3 mm. follicle was found in her right ovary.

A record of puberty in another rhesus macaque is incorporated in the account of Dr. C. Dobell's monkey given on p. 703. In this monkey the sexual skin became active one month before the first menstruation.

There are at present in the London Gardens two young female rhesus macaques, the one (S) weighing 3·8 kg., the other (B. S.) 3·7 kg., both of whom have passed puberty (judged by the occurrence of menstruation and sexual skin changes). Both are in the same stage of dentition, which corresponds to that of a girl about eight years (the only permanent teeth which have erupted are all four incisors in the lower jaw, the two central incisors in the upper jaw, and the four first molars).

Apart from these records of rhesus macaques, I have had the opportunity of making observations on puberty in a limited number of other sub-human primates. A female chimpanzee (S), which arrived in the London Zoological Gardens on November 10th, 1927, began to show variations in the prominence of her perineal area in June 1929. Since then there have been from time to time perceptible differences, insufficiently marked to record, in the degree of turgidity of her perineal area. Her perinæum is permanently more prominent now than it was six months ago. Her weight on 20th January was 22·7 kg. Her dentition on that date was as follows:—all the permanent incisors and the first and second permanent molars in each jaw. Only one milk tooth remaining, a lower canine.

A second chimpanzee (B), which arrived in the Gardens on August 27th, 1927, has as yet shown no variation in the conformation of the perineal area. Her weight on the 20th January was 20·4 kg. Her dentition on this date was as follows: permanent teeth, four first molars, lower central incisors, one upper central incisor cutting; the rest of her teeth were deciduous.

A pig-tailed macaque, weighing 5 kg., first showed signs of activity of her sexual skin in January 1930. Menstruation has not yet occurred. All her permanent incisors and first and second molars have erupted. This is not the human order of eruption, but the animal would correspond in age to a girl of about nine.

The records of puberty in two mangabeys has been quoted on p. 701. In one, activity of the sexual skin was manifest for about one month, in the other, for two months, before menstruation occurred.

A young drill, *Mandrillus leucophaeus*, first showed signs of activity of her perineal area on the 27th November, 1929. Her weight on this date was 6·6 kg. Her teeth were deciduous except for permanent first molars and permanent incisors, which had already erupted. Her sexual skin quickly reached a condition similar to that of the mangabey's when active (see p. 700), except for a slight groove between the clitoric and vulval portions. The true perinæum—*i. e.*, the area between the fourchette and anus—is most affected. The size of the entire swelling is approximately 4 inches long, 2½ inches broad, and about 1½ inches deep. It has varied slightly in size, but on the 30th January, 1930, was almost the same as in the first week in December 1929. According to a keeper, vaginal bleeding occurred on the 22nd of January. I was unable to verify this observation.

These histories indicate that in the monkey sexual maturity begins with activity of the sexual skin. This activity does not attain adult proportions at once, and is maintained for one or more months. Menstruation follows usually after the sexual skin has become inactive. The ovarian changes of puberty have not been investigated, but external appearances suggest that more than one follicle ripens, only to become atretic and to be followed by others. Whether ovulation invariably precedes the first menstruation is unknown. The cause of the irregularity of the earlier cycles is also unknown.

Judging by dentition, puberty is reached relatively earlier by the sub-human primate than by the human.

VIII. Pregnancy and Lactation.

Apart from recent publications, the most valuable record of pregnancy in primates is Breschet's 'Gestation des Quadrumanes,' 1845. Breschet quotes from

a letter of Geoffroy-Saint-Hilaire the number of monkey pregnancies that had occurred in France up to 1845. According to the latter investigator it is impossible to determine accurately the duration of pregnancy, as monkeys continue to copulate after conception, though usually not for long. "Lorsque les femelles sont pleines, elles sont beaucoup moins recherchées des mâles, qui souvent même les repoussent et les maltraitent. Il arrive alors tout naturellement que les femelles évitent les mâles. Ce changement dans les habitudes des animaux et la non-réapparition des règles indiquent, longtemps avant le dévelloppement du ventre, l'état de gestation des femelles." According to Geoffroy-Saint-Hilaire gestation in monkeys lasts approximately seven months.

Among more recent records of pregnancy and lactation in sub-human primates are those of Pocock (1906), Von Allesch (1921), Montane (1915, 1928), Fox (1929), Lucas, Hume, and Smith (1927), and Hartman (1928–1929). These will be briefly considered.

An orang gave birth to a male baby in the Philadelphia Gardens on September 25th, 1928 (Fox, 1929). Pregnancy was first suspected in January 1928. "Early in March some slight swelling in the vulvar region was noted, and this remained stationary until during July, when it began to increase steadily." Unfortunately, Fox does not state whether the amount of swelling was equal to that which occurred in the non-pregnant condition. This female did not eat the placenta, though she had bitten into it.

Fox also records the birth on October 1st, 1928, of a male chimpanzee in the same Gardens. The menstrual history of the mother was apparently unknown. In fact, she was not known to be pregnant. Like the orang, this chimpanzee did not eat the placenta; nor did she nurse her baby, which was removed after two days and artificially fed. Four days after giving birth she copulated. Further reference to this animal will be found on p. 698.

The period of gestation in the chimpanzee is probably nine months (Yerkes, 1929).

Montané's record of pregnancy has already been noted (p. 698). The chimpanzee ("Cucusa") observed by him lost blood, without the occurrence of pudendal turgescence, sixteen days after delivery. The same female menstruated for the first time eighteen months after parturition; another chimpanzee after twenty-one months. Montané notes that "all signs of catamenia disappeared during the last three months of pregnancy" in the female already mentioned on p. 698 (Yerkes, 1929). Yerkes (1929) also quotes von Allesch (1921) in support of the view that the chimpanzee continues to menstruate during the early part of pregnancy.

Yerkes records a remarkable observation, apparently on the authority of Madame Abreu. Though chimpanzees continue to copulate during pregnancy, "following the birth of the young and until the baby is weaned and the production of milk ceases, there is no relation whatever between the animals." This observation is supported by Bingham (1928).

Lactation in the chimpanzee lasts, according to Yerkes, "perhaps for a year or two". This estimate is probably too short. An adult female orang was purchased by the Zoological Society of London on 21/1/28. When she arrived she was nursing a "baby"; it was only on very rare occasions that the "baby" was seen outside her arms, and he was usually sucking. Whether or not she was lactating, it is impossible to tell. The "baby" died of tuberculosis two months after its arrival. It had a complete set of milk teeth and, in addition, the first permanent molars. From analogy with the chimpanzee (Zuckerman, 1928) its age was five or six years.

It is significant that accounts of the pregnancies of at least two chimpanzees do not contain any reference to swelling of the sexual skin, which Fox describes in the pregnant orang. All published records of pregnancy and lactation in anthropoids

are, however, so vague and contradictory that no great value can be attached to any of the recorded "facts"*.

A clearer view of pregnancy in sub-human primates can be obtained from records of monkey births.

Pocock (1906) writes that gestation in the Pig-tailed Macaque (*Macaca nemestrina*) is "not more than seven and not less than six months." (This is the length of time gestation is said to last in almost all monkeys.) He records that menstruation did not occur during the pregnancy of a Pig-tailed Macaque, but does not note whether activity of the sexual skin continued. He does, however, mention that a male with whom she shared her cage did not copulate with her, and considers that the male monkey's "disregard for the pregnant female was due to her condition. This may have brought about some subtle change in her, a difference or deprivation of odour may be, which perhaps robbed her of an attractiveness she might otherwise have held for him." I myself have no doubt that this disregard was due to lack of activity of her sexual skin. This female did not devour the placenta after parturition.

Pocock gives a record of lactation in a macaque lasting 7–8 months. The interval which elapses before the young supplements its diet with solid food is, however, far shorter.

Heape (1894) noted that the sexual skin of the rhesus macaque (*M. mulatta*) is highly coloured during pregnancy, and this observation has been corroborated by Hartman (1928 *e*), who writes that "a most brilliant sex color was also maintained during the entire gestational period and for several weeks after parturition." No mention is made of swelling. Fifteen gestations which have occurred in Hartman's colony of rhesus macaques varied from 149 to 174 days in duration, the average being 164·3 days. It would seem that gestation is usually a few days longer in primipara than in multipara.

Hartman has described in several of his papers "the placental sign of pregnancy". This consists of a "leakage of blood into the uterine lumen and thence into the vagina" occurring "from the thirteenth to the twentieth day after the assumed date of conception" (1929 *b*). Corner draws attention (1923 *a*) to a similar occurrence in the human uterus in the early stages of pregnancy.

Pregnancy is usually overlooked in monkeys unless close watch is kept for vaginal hæmorrhage. One morning in November 1928 a female rhesus in the London Zoological Gardens was found dead. She had been perfectly well the night before. Death was due to hæmorrhage from a central placenta prævia, brought about by the opening of the internal os in the first stage of labour. (A full description of this monkey is in preparation.) Pregnancy had not been suspected.

An adult female Pig-tailed Macaque, *Macaca nemestrina*, in the London Gardens, gave birth to a baby on July 15th, 1928. Although neither swelling of the sexual skin nor menstruation had occurred for some months previous to this (testimony of keeper), she was not considered pregnant. She had copulated frequently with an adult male of the same species, with whom she had been for seven months previous to parturition. They were separated from each other on the day of the birth. The baby continued to suck for nearly a year, though it cannot be said for certain that the mother was lactating for this length of time. Four weeks after his birth the baby began to eat solid food.

On p. 706 I noted that the first signs of activity of the sexual skin of this female occurred eight months after the birth of her baby, and that she menstruated two months later. Since then she has had five cycles differing from

* Savage and Wyman reported perineal swelling in pregnant and lactating chimpanzees (see p. 697). The "folds" they describe may well have been the "residuum of swelling" met with, for instance, in baboons (see p. 714).

each other in length and external signs (see Chart 3, p. 707). During the last cycle she probably became pregnant. Her sexual skin no longer becomes active. She continues, however, to copulate with her male. If she is pregnant it will be possible to estimate the length of gestation fairly accurately, for the last subsidence of swelling coincided with the rupture of the follicle whose ovum was fertilised (see p. 721).

I have kept records of seven pregnancies in hamadryas baboons occurring during the past 2½ years.

The first is the female (M) noted on p. 711. I did not record her pregestational menstrual history, and therefore cannot estimate the duration of her gestation. Her baby continued to suck for nine months. During pregnancy and lactation (except for one occasion) her sexual skin was inactive.

The second is a female (Sm.) who was observed through one cycle (I began to keep records during the stage of pudendal enlargement). After the subsidence of this swelling no further sexual skin activity occurred for approximately 9½ months. She gave birth to a male baby 185 days after the subsidence of swelling; as indicated on p. 721, one may infer that the ovum fertilised was the one liberated by the follicular rupture which coincided with the last observed subsidence of swelling. Gestation therefore lasted 185 days—or perhaps one or two days less, as it is impossible to state whether the ovum was fertilised the day it was liberated, or a day or two later. With the exception of a slight degree of prominence of the preputial sheath towards the last few weeks (this was noted in two of the other pregnancies), the pudendum was at its most shrunken level throughout pregnancy. (This was the condition observed in all these pregnancies.) The colour of the sexual skin varied. It was occasionally bright red. There was but little lochia after parturition. This female's baby died after 99 days, during which time the sexual skin was altogether quiescent. Ten days after its death the sexual skin began to swell. No obvious bleeding preceded this swelling. I cannot, however, state definitely that none occurred (see Chart 5, p. 712).

The third is a female (Sc.) whose pregnancy, judged by the same standards, lasted 162 days. Her baby lived 64 days. Ten days elapsed before the sexual skin commenced to swell. This was not preceded by external bleeding (see Chart 6, p. 712).

The fourth animal (Ha.) died on the 173rd day of her pregnancy (see Chart 7, p. 712). A full-term fœtus was found *in utero*. A description of this animal will be submitted in another publication.

The fifth (Sp.) gave birth after a pregnancy lasting 154 days. The baby died the day after its birth. Her sexual skin began to swell 20 days after parturition (see Chart 8, p. 713).

Pregnancy in the sixth (Scr.) lasted 171 days. Her baby died after 19 days. The sexual skin became active 11 days after its death (see Chart 9, p. 713).

The seventh (Wa.) is a female whose conception date—she is judged pregnant on the evidence of the other pregnancies, *i. e.* cessation of menstruation and non-occurrence of external changes—was 5th November, 1929. She is still pregnant (see Chart 10, p. 713).

The average length of gestation in the five whose complete histories are recorded is 169 days; the range 154–185 days. These figures are remarkably similar to those of the rhesus macaque Hartman has recorded (p. 734). The five baboon pregnancies were altogether similar in their main features. The sexual skin was quiescent throughout gestation and for the duration of lactation, showing signs of activity from 10–20 days after suckling ceased. The inference that may be drawn from these facts will be discussed below. In all the pregnancies that have occurred on the Monkey Hill since it was established in 1925, the placenta has been eaten. Copulation was observed very rarely—in some cases not at all—

during pregnancy. It has been observed no more frequently during lactation, when the sexual skin is quiescent.

On p. 705 I recorded a pregnancy in a *Macaca radiata*, owned by Dr. C. Dobell, F.R.S. Further details about this animal are as follows. Gestation lasted about 150 days. After the first month of pregnancy she refused to copulate. The baby was born overnight and found dead, attached to cord and placenta, next morning. The mother's mammary glands did not enlarge until 24 hours later, and she had milk—in diminishing quantity—for about three weeks. The lochia continued for a week. The first time she copulated was 47 days after the birth of her baby, and she menstruated 2 days after this.

Details of pregnancy in the marmoset are noted on p. 717. Miss Hume also tells me that the time that elapses after parturition before a female will pair is variable. It has been observed after 23, 34, and 45 days. After a miscarriage only 12 days elapsed. Young marmosets begin to eat solid food when about 25 days old, though they continue to suck for a much longer period.

It is generally believed that women may very occasionally continue to menstruate after the beginning of pregnancy, and it is said, on somewhat doubtful grounds, that menstruation is theoretically possible until the decidua capsularis has developed sufficiently to fuse with the decidua vera over the whole uterine cavity, that is, until the end of the third month. It is exceedingly doubtful, however, whether the vaginal bleeding that is observed in pregnant women can ever be truly said to represent normal menstruation.

Both Montané and von Allesch have reported vaginal bleeding during pregnancies of chimpanzees. Montané's description, as already pointed out, is somewhat vague, and possibly faulty in certain respects. Von Allesch's observations appear more accurate, but confirmatory evidence is necessary before one assumes bleeding in pregnancy as a normal occurrence, or that it represents menstrual bleeding. Cuvier has also left a record of a macaque which "menstruated" as late as three months before parturition. These statements, however, are outweighed by Hartman's careful observations. As has already been mentioned, Hartman found that the only bleeding in the pregnant macaque was that occurring from the 13th to the 20th day from the assumed date of conception, and referred to as the "placental sign". Cyclical menstruation would therefore appear to be as suppressed during pregnancy in sub-human primates as it is in women.

Because of Hartman's records of the maintenance of sex colour throughout pregnancy in the rhesus macaque, it is impossible to tell with certainty whether or not all cyclical ovarian activity is then in abeyance. The uniform maintenance of sex colour would, however, suggest uniform œstrin secretion. This is in agreement with the fact that the body fluids of the pregnant lower mammal contain the hormone in abundance. Parkes (1929) has discussed this fact critically, suggesting that, in spite of the abundance of the follicular hormone during the luteal phase (pregnancy), the corpus luteum may still be dominant. The follicular hormone, for instance, does not produce œstrus or abortion, or give any signs of its presence during pregnancy in the lower mammal. In the pregnant rhesus macaque, however, it does lead to coloration of the sexual skin, though not cyclically as in the non-pregnant female.

On the other hand, the pregnant or lactating baboon does not menstruate or show pudendal swelling—that is to say, the last subsidence of swelling which one observes previous to parturition represents the end of the baboon's non-pregnant state or, alternatively, the beginning of her pregnancy. Almost certain proof of this is that the duration of gestation in the baboon, estimated according to this basis, agrees closely with the duration of pregnancy in the rhesus macaque as estimated by Hartman by a different method (controlled matings and vaginal smears). The follicular hormone, œstrin, does not, therefore, cause any change in the sexual skin of the pregnant baboon apart from a slight colour change difficult

to estimate. It is therefore doubtful what significance must be attached to the reported occurrence of pudendal swelling in a pregnant orang (Fox 1929. See p. 733). The fact that swelling does not occur in the pregnant baboon, though sexual skin colour may be intensified, is suggestive that these two characteristics vary independently of each other. This, too, was suggested by certain of Allen's experimental findings (see p. 722).

The problem of the occurrence of external changes due to the follicular hormone in the pregnant macaque is very complicated, and further data are essential before definite conclusions can be reached. It is closely bound up with the problem of the significance of the occurrence of œstrin in all mammals during pregnancy. Moreover, the possibility that sexual skin swelling and sexual skin coloration vary independently of each other must be carefully investigated. Hartman, while he notes the reddening of the sexual skin of the pregnant rhesus monkey, does not mention swelling.

The desire for copulation in the female is, as I have already noted, related to swelling of the sexual skin. Whilst sexual skin changes are in abeyance during pregnancy and lactation, baboons seldom copulate. Moreover, the greater number of accounts indicate that the same is true of most primates. When copulation does occur during these phases, responsible factors may be unnatural conditions and confinement in pairs. Under natural circumstances copulation probably takes place seldom, if at all, during these phases.

Pocock writes (1906) that "devouring the placenta by the mother seems to be the invariable rule in all species of Mammalia, with the exception of Man." In this section I have noted all those instances where monkeys have been recorded as failing to do so. Such occasions, however, are rare compared with those when the reverse happens. Nothing seems to be known of the rationale of this behaviour, but the old suggestion that the placenta is a galactogogue is, as Hartman points out (1928 *e*), fairly well founded.

No external signs of the menstrual cycle are obvious while the baboon and pig-tailed macaque continue to secrete milk. Lactation in the pig-tailed macaque lasts little more than six months.

When lactation ceases abruptly, for instance on the death of a baby, or, when it does not begin at all, as when the baby is born dead or dies soon after birth, a short interval elapses before a menstrual cycle starts. This interval varies from 10 to 20 days (p. 735).

From all these facts one may infer that during gestation and lactation in monkeys follicular changes are usually suppressed. When there is no functional need for the continuation of lactation, a few days elapse before a menstrual cycle begins, with signs of activity of the sexual skin.

IX. Changes in the Ovary and Accessory Organs.

(1) *Ovaries and Uterus.*

From Heape's classical studies of *Pithecus entellus* (=*Semnopithecus entellus*) (1894) and *M. mulatta* (=*M. rhesus*) (1896) one learns that the primate uterine cycle may be divided into the following stages:—

A. Period of Rest.
B. Period of Growth.
C. Period of Degeneration.
D. Period of Recuperation.

During the period of rest, the mucosa, formed of a single row of cubical cells, is of "remarkably even consistency throughout". The blood vessels in the mucosa are small. During the period of growth, the stroma gradually increases in density, the blood-vessels beneath the epithelium increase in size and number and become

more congested, while the epithelium becomes thinner. In the period of degeneration the mucosa swells still further, the numerous and dilated blood-vessels in the comparatively open tissue beneath the epithelium rupture, the epithelial cells increase in size and degenerate, so that the lacunæ formed by the rupture of the sub-epithelial vessels burst, and free blood fills the cavity of the uterus. Finally, "all over the body and fundus of the uterus the superficial portion, about one-third, of the mucosa, including uterine and glandular epithelium, stroma and blood-vessels, is cast away." The period of recuperation begins, before the menstrual clot is expelled from the uterus, with the reformation of epithelium, partly from the torn mouths of glands, and partly from the stroma cells. In this stage the blood-supply is reduced and new capillaries are formed.

It is difficult to gauge from Heape's data the exact relationship of the ovarian to the uterine cycle. Heape himself was mainly interested in the correlation between menstruation and ovulation. In all his monkey specimens he found only one instance where "a recently discharged follicle was found in the ovary of a menstruating *Macacus rhesus*" (1896). He therefore considered the two processes to be distinct, though he remarked that during the pairing season "ovulation may be more frequent, and may more often be coincident with menstruation." He was able, however, to show definitely that there are cycles in which ovulation does not occur at all. The endometria of those animals in which he found ripe corpora lutea had the appearance characteristic of the end of the period of growth and the beginning of the period of degeneration—periods which can to-day be referred to as the luteal phase of premenstrual congestion and the period of menstruation respectively.

Van Herwerden (1906) investigated the uterine and ovarian cycles in *Macaca irus* (= *Cercocebus cynomolgos* = *Macacus cynomolgos*). Her results were remarkably similar to those of Heape. She did not find, however, that the uterine epithelium was regenerated from stroma cells. She was able to demonstrate successfully that in cycles when ovulation did not occur premenstrual uterine changes were less marked than when it did occur. Moreover, she believed that the uteri in her collection in which menstruation had occurred without ovulation, *i. e.*, uteri with low endometrium and short straight glands, were from animals killed in the non-breeding season.

Both Heape and Van Herwerden classified the material they investigated without reference to the stage of the cycle at which their animals had been killed. Corner (1923 *b*) was the first to study the ovarian and uterine cycles in animals which had been observed alive for some while and then killed at particular stages of the cycle. His observations on cycle lengths of *M. mulatta* have been noted on p. 702. From a study of 11 monkeys he was able to show that "macaques at times menstruate without ovulation." When ovulation did occur it took place about 12 to 14 days before the expected onset of menstruation. The endometria of two monkeys, one killed 9 days, the other 18 days, after the onset of menstruation, and both showing retrogressive stages of the corpus luteum, and the endometrium of another monkey killed 12 days before the expected onset, and showing a very early corpus luteum, were all of the "interval" type—(Heape's resting stage). The endometrium of a monkey killed 10 days before the expected onset of menstruation and showing an almost completely organised corpus luteum was passing into the "premenstrual" type—Heape's "growth" period—while that of a monkey killed 7 days before the expected onset and showing a solid corpus luteum, was distinctly "premenstrual"—*i. e.*, "the surface epithelium is high, the glands are distinctly spiral in form, there are marked secondary projections into the glands, the glandular epithelial cells are high and their surfaces frayed, and the basal glands are increased so much that the endometrium appears on section to be of spongy texture."

Corner notes that the endometrium of the animal killed 12 days before the

expected onset of menstruation, and just after ovulation had occurred—the ovum was found in the Fallopian tube—showed none of "the characteristic changes which mark œstrus" in the pig, rat, mouse, or guinea-pig; that is to say, there were no signs of endometrial degeneration such as vacuolar degenerations of the epithelial cells or an accumulation of leucocytes under the epithelium. This extremely important observation will be referred to again in the discussion at the end of this paper.

The maximum size of the resting follicle of *M. mulatta*, is, according to Corner, 1·5 to 2 mm.; that of the mature follicle 4 mm. In the lower mammal "the maturation of the follicle and its enclosed ovum... are terminal events, progressing with great rapidity in the last days or even during the last hours before rupture."

Six of Corner's animals, though they were all killed within 17 days after menstruation, showed no signs of ovulation, either recent or impending. Three of these appeared "to have been menstruating with an interval endometrium." Another, however, "showed traces of having passed through a premenstrual stage."

In 1927 Corner summarised the theory of the human reproductive cycle based on the work of Fraenkel, Hitschmann & Adler, Meyer, and Schroeder. "Ovulation is a periodic function occurring regularly at about the middle of the interval between two menstrual hemorrhages. It is followed by the development of a corpus luteum at the site of the discharged follicle; and this structure, acting as a gland of internal secretion, causes changes in the endometrium (the well-known 'premenstrual' changes first described by Hitschmann and Adler) by which it is prepared for implantation of the embryo. If the ovum is fertilized the 'premenstrual' endometrium thus becomes the endometrium of early pregnancy. If, however, the ovum is not fertilized, the corpus luteum retrogresses, and at about the same time the 'premenstrual' endometrium suddenly breaks down with resultant hemorrhage. Menstruation is on this theory merely a violent demolition of the 'premenstrual' uterine edifice, some days after the expected tenant (the embryo) fails to arrive. Each menstrual period is therefore necessarily dependent on the occurrence of ovulation about two weeks before."

In this paper, however, Corner provides additional evidence that the previous occurrence of ovulation is not essential for menstruation. One animal (Macaque 15) was found to be menstruating from a typical "premenstrual" endometrium; laparotomy had shown that she had ovulated about fourteen days before. Another (M. 10), whose vaginal smear history was identical with that of M. 15, was found to be menstruating from an "interval" endometrium; this animal showed no signs that ovulation had occurred during the preceding two or three cycles. Laparotomies on other animals also showed that menstruation might occur without previous ovulation. "Out of about twenty-seven cycles of which something is definitely known, from autopsy or exploration, ovulation has occurred in seven only.... Histologically there are two types of menstruating endometrium—one showing 'premenstrual' changes, the other devoid of them, according to the occurrence or non-occurrence of ovulation twelve or fourteen days beforehand."

Corner's findings have been confirmed by both Allen and Hartman. The recovery of shed ova by the former (1927, 1928 *c*) "extends the range of the period in the menstrual cycle during which ovulation may occur to the tenth to the fourteenth day following the first day of the preceding menses" (1927). In Allen's monkeys ovulation occurred in less than fifty per cent. of the observed cycles. On p. 719 I gave an account of some of Hartman's observations on a monkey whose persistent sexual skin coloration was found to be associated with a cystic follicle. Seven days after this follicle was artificially ruptured the animal menstruated from an "interval" endometrium (1928 *a*).

Allen has made extensive studies of the effects of the follicular hormone, œstrin, upon the endometrium. The cervix of a spayed female under the influence

of injected œstrin increases enormously in size relative to the control cervix of a spayed female, and its glands become heavily infiltrated with leucocytes. A corresponding amount of growth is induced in the body of the uterus of a spayed female. Leucocytes are rare in the stroma and apparently not met with under the epithelium. However, even though the glands in some regions had "begun to assume the tortuous corkscrew appearance interpreted in the premenstrual uterus as a sign of growth," the largest amount of growth induced was only "equal to the normal just after ovulation" (1927). "Even after long series of injections, however, it was not possible to obtain full premenstrual development of the endometrium" (1928 *d*). Following the cessation of injections the uterus soon diminishes in size, in five days approaching in size that of the control spayed female. The similar result obtained by Robertson (1929) with a combination of œstrin and corpus luteum extracts has been noted on p. 719.

(2) *The Vagina.*

According to Corner (1923 *b*) there is in *M. mulatta* a tendency to "a cyclic variation of the vaginal contents, although far less sharply defined than that seen in rodents." In the first half of the cycle there are relatively few epithelial cells and relatively more leucocytes. About the middle of the cycle leucocytes diminish in number. They sometimes reappear a few days later, but "more often they were absent until the onset of menstruation or a few days before." They were always present during menstruation. In the latter half of the cycle, "when the leucocytes were few or absent, there was usually an increased desquamation of epithelial cells." Corner correlates the drop in the leucocyte count about the middle of the cycle with the occurrence of ovulation at that time, and compares this with the similar absence of leucocytes in the œstrous smear of the rodent.

The source of the leucocytes in the vaginal secretion is the cervix uteri and the upper vaginal epidermis. The mucosa of the uterus proper is not involved.

The vaginal smear records of two of Corner's monkeys (macaque 15 and macaque 10) were identical, even though the one was undergoing cycles with, and the other without, ovulation (1927).

Allen (1927) obtained results similar to those of Corner with the same species of monkey. "During the latter half of the second and third week of the cycle the epithelial elements were present in greatest numbers and often completely cornified; non-nucleated cells appeared at these times. Leucocytes were present in greatest numbers before, during and after menstruation, and in least numbers or absent between the tenth and the twentieth to twenty-fourth day of the shorter cycles." Injection of œstrin into spayed females resulted in "decrease in number and final disappearance of leucocytes and increase in the number of epithelial cells typical of the interval in normal cycles." "Extreme" growth is induced in the vaginal wall, and cornification may be produced. Leucocytes reappear in the vaginal contents a few days after cessation of injections, having infiltrated the stroma.

Considering that Corner has stated the source of the vaginal leucocytes to be both the cervix and the upper vagina, it is difficult to understand why œstrin injected into a spayed female should produce a heavy leucocytic infiltration in the cervix (see above) and at the same time a disappearance of leucocytes from the vaginal smear and from the vaginal wall.

Hartman (1928 *e*) has employed the vaginal smear technique in estimating the fertile period of the cycle for mating experiments, and has found that the most fertile stage occurs before the leucocyte count has reached its minimum.

In 1928 (*f*) he discovered that a small number of red blood cells may be recovered in lavages made from the macaque vagina at times other than

menstruation*. These cells could only be recovered between the eleventh and eighteenth day of the cycle. "The blood could hardly originate, as in dogs and cows in the procestrum, from a congested uterus, since the red blood cells were recovered only for a very short time—one or two or at the outside three days—whereas the premenstrual congestion increases progressively towards the succeeding menses. This leaves only one other important event occurring in the interval, namely, ovulation." Laparotomies were made on two females mated at the fertile period of the cycle, judged by leucocyte counts and sex colour. In one, red blood corpuscles were found in the vaginal smear. Laparotomy showed a recent rupture. In the other none were found. Laparotomy showed that she had not ovulated. Hartman therefore concluded that the erythrocytes were derived from the slight hemorrhage accompanying ovulation. In a later publication (1929 *c*), however, he reconsidered this view and stated that "the intermenstrual bleeding is uterine and not ovarian in origin." More than 75 per cent. of 105 menstrual cycles observed at a favourable time of the year showed this "interval bleeding". Twenty-three additional laparotomies are described in this paper. Two of these, though performed on females with red blood corpuscles in their vaginal smears, showed neither a corpus luteum nor a large follicle in either ovary. According to Hartman, these two cases "are therefore exceptions to the rule"—*i. e.* intermenstrual bleeding is associated either with recent ovulation or the presence of a ripe follicle. Hartman also notes in this paper that "mid-interval" bleeding may be found at any time from the seventh to the eighteenth day of the cycle, and that it may last for a considerable time—in one monkey it lasted from the eighth to the eighteenth day. These facts strongly suggest that the bleeding is not ovarian in origin; they do not, however, prove that it is uterine. Further reference will be made to this problem later.

I attempted to follow the vaginal cycles of an Anubis Baboon (*P. anubis*) and a Yellow Baboon (*P. cynocephalus*). Smears were obtained through the wire of their cages on alternate days without restraining the animals in any way.

As I mentioned on p. 729, the keeper who obtained these smears usually found that the animals would not allow the passage of a spatula during the resting stage of the sexual skin in the latter half of the cycle. After about 1½ months they refused to "present" even when their sexual skins were swollen.

Enough smears were made, however, to show that the vaginal cycle of the baboon is similar to that of the macaque. Leucocytes are usually absent altogether about the middle of the cycle, and appear a few days after the subsidence of pudendal swelling. They are present during menstruation and during the early part of the phase of pudendal swelling. Epithelial desquamation is greatest about the middle of the cycle when leucocytes are absent. Non-nucleated epithelial cells are then numerous.

The vaginal cycle of an Abyssinian Cercopitheque (*Cercopithecus æthiops*) was followed for nine months. Smears were made approximately every second day. The vaginal changes in this animal are the same as in the Rhesus Macaque. Leucocytes are most numerous before, during, and after menstruation, and frequently entirely disappear from the smear about the middle of the cycle. Epithelial desquamation is greatest at that time, and non-nucleated epithelial cells numerous.

Red blood corpuscles were not seen in any of the smears of these three monkeys except at the menstrual periods.

(3) *The Mammary Glands.*

The normal cycle in the primate mammary gland does not appear to have been investigated. Allen (1927) has shown that œstrin injected into spayed females

* There is no record of any similar finding in Allen's or Corner's work; their vaginal smear technique was, however, different.

produces marked growth, branching of ducts, and increase in the number of alveoli. The same result is obtained with immature females (1928 *e*).

X. Discussion.

Various attempts have been made to explain the primate menstrual cycle and to homologise it with the œstrous cycle of other mammals.

The clinical view of the human cycle that "women menstruate because they do not conceive" is explained fully in the quotation from Corner on p. 739. Though it depends for its support upon recent work, it is by no means new, for, according to Marshall (1922), it was expressed at least as early as 1871 by Sigismund. One of its main limitations, as Corner pointed out, is that it conflicts with the fact that menstruation may occur, in both monkeys and women, without the previous occurrence of ovulation and the consequent formation of a "premenstrual" endometrium. An equally serious limitation is its complete disregard of the occurrence of a follicular phase in the cycle. The follicular hormone œstrin occurs without any doubt in the human ovary and placenta (Allen, Pratt, and Doisy, 1925). No theory which ignores its occurrence can be sound.

On the other hand, Heape's view (1894, 1900) that menstruation is the same as the pro-œstrous destruction which precedes œstrus in the bitch is equally untenable, since it completely neglects the occurrence of a luteal phase in the human cycle. (The luteal phase or pseudo-pregnancy, was, of course, not recognized in the cycle of the bitch until 1909, when it was described by Keller.)

Heape identified the pro-œstrous growth in the bitch uterus with the growth-phase of the monkey endometrium, and the pro-œstrous degeneration of the bitch with menstruation. This homology he described as "absolutely certain" (1900). The œstrus which follows pro-œstrous degeneration in the bitch was paralleled by a period of heightened desire which, according to Heape, many women experience after menstruation.

Marshall (1905) at first accepted Heape's interpretation. Later (1917), however, after a study of the post-œstrous changes in the non-pregnant bitch, he modified Heape's interpretation, writing that it seemed possible "to regard menstruation in Man as representing pseudo-pregnant destruction as well as pro-œstrous degeneration."

He reiterated the same view in 1922. "It is possible . . . that in Man the breaking-down stage represents pseudo-pregnant degeneration as well as pro-œstrous destruction owing to the two processes having become telescoped into one another as a consequence of the shortening of the cycle." He discussed the problem more fully in 1927. After referring to Heape's view that menstruation in the Primate represents pro-œstrous destruction in the bitch, he continues:—"The most recent observations have shown that ovulation in Man takes place on or about the fourteenth day after the beginning of the menstrual flow, and that from that time onwards till the end of the cycle the uterus undergoes growth-changes comparable to what occur in the lower mammals during the abbreviated pseudo-pregnancy. . . . Degeneration of the corpus luteum is seen on the last day of the cycle—that is, the day before the beginning of a new menstrual discharge. These facts point to the conclusion that the menstrual discharge may take place (partly, at any rate) as a result of the regression of the corpus luteum. . . . During the pro-œstrum in the bitch . . . the growth of the endometrium is slight as compared with the hypertrophy which takes place in the premenstrual period in Man. These facts, taken in conjunction with the observation that the bitch experiences pronounced pseudo-pregnant hypertrophy in correlation with the development and persistence of the corpora lutea at a later stage in the cycle, indicate that the proœstrous processes in the bitch represent something less than the complete menstrual phenomena in Man. . . . Heape had previously shown (1897) that

menstruation may occur in the monkey without being in any way associated with ovulation. In such cases the menstrual phenomena are probably to be regarded as purely pro-œstrous in character, *and comparable to the congestion and bleeding which occurs at the beginning of the heat period in the bitch* *. Moreover, it seems likely that the menstrual processes in Man may in certain individuals be of a similar character. On the other hand, in most individuals, both with monkeys and Man, whereas the constructive changes (which have been described as usually occurring in a marked manner) represent an abbreviated pseudo-pregnancy, it is probable that the destruction which supervenes is the equivalent of pseudo-pregnant and pro-œstrous degeneration telescoped into one period owing to the shortness of the cycle." He concludes, "The natural inference is, therefore, that the menstrual discharge in Man and monkeys represents pro-œstrous destruction, often accentuated (as above suggested) by pseudo-pregnant degeneration."

Clearly, therefore, Marshall looks upon menstruation as representing the breakdown of the pro-œstrous growth which heralds the succeeding ovulation combined with (in his words "telescoped into") the breakdown of the pseudo-pregnant growth which followed the preceding ovulation.

This view is open to at least one very serious criticism. It has been shown clearly in the present paper that the follicular phase (pro-œstrus) in primates extends throughout the earlier half of the cycle. According to Marshall's theory, however, this phase comes to an end at the very beginning of the cycle. Moreover, according to Marshall's view, an interval of about ten days at least must elapse between the end of pro-œstrus and the ovulation of which it is the forerunner: this is extremely improbable. Nevertheless, as I hope to show later, menstruation may represent both pro œstrous degeneration and pseudo-pregnant destruction, though not combined in the manner suggested by Marshall.

Allen (1927) has suggested that "menstruation is due to an absence of follicular hormonal stimulus after the hormone has been acting for a certain period of time." He found that double ovariectomy performed on *M. mulatta* towards the end of, or immediately after, the follicular phase of the cycle (as judged by the colour of the sexual skin) was followed by "apparently typical menstrual bleeding" five to thirteen days before the expected onset of menstruation †. He explained the fact that in monkeys menstruation is normally delayed for some two weeks after ovulation as being due to the possible continued secretion of œstrin by the corpus luteum. He also suggested that the secretion of the follicular hormone by the placenta and its continued action explain the absence of menstruation during pregnancy. In short, he assumed that the follicular hormone is responsible for all the changes of the menstrual cycle and for those of pregnancy.

There are several objections to this point of view. As Parkes points out (1929), it is "unlikely that the corpus luteum itself, an organ whose development is always associated with the absence of œstrus, would produce the œstrous hormone." Furthermore, it is a fact that the appearance of the next menstruation is not hastened in those cycles in which ovulation does not occur, and in which, therefore, no corpus luteum is formed. Also it is now known that ovarian and *indirectly* uterine periodicity is under the control of the anterior pituitary, which acts upon the uterus *through the ovaries* (see Parkes, 1929, and Fee & Parkes, 1929). When

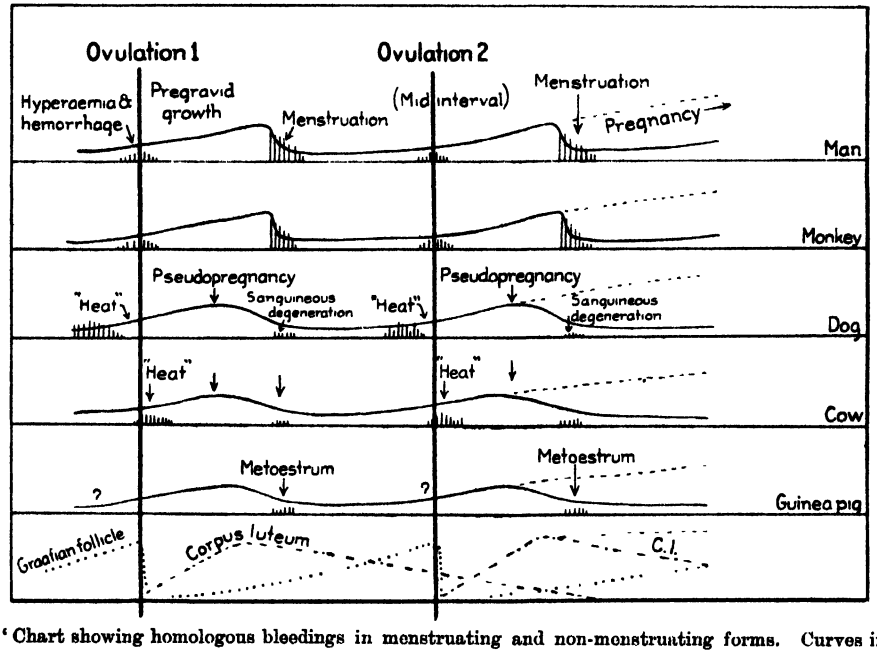
* Italics ours.

† Allen also cites a case where, instead of ovariectomy, an ovary was pierced and aspirated on the 16th day of the cycle, leading to the appearance, on the 6th day after the operation, of bleeding, which lasted 6 days. He assumes that menstruation was hastened by the operation. This is, however, doubtful.

The length of the operative cycle was 22 days. The same animal had previously experienced normal cycles of 25 and 26 days, and, following the operative cycle, went through cycles of 18, 19, and 20 days' duration. As almost all observers have recorded normal cycles in *M. mulatta* as short as 22 days, and as this animal of Allen's experienced normal cycles almost equally short, it cannot be said that the injury to the ovary hastened the appearance of menstruation.

the latter are removed, therefore, the normal regulation of the cycle is disturbed, and the results obtained from an ovariectomised animal may not be at all comparable with the events of a normal cycle. Moreover, Allen's own observation that œstrin alone is not sufficient to induce premenstrual growth of the endometrium (see p 740) indicates that œstrin is not the sole controlling factor of the menstrual cycle. He himself admits later (1928 *d*) that "perhaps additional hormonal stimulus (either in amount or in time) or some other hormone qualitatively different, possibly from the corpus luteum, may be required" to produce the premenstrual endometrium.

Diagram 2.



"Chart showing homologous bleedings in menstruating and non-menstruating forms. Curves in solid lines: growth and involution of the endometrium. Bottom lines (dotted): growth and decline of the graafian follicle and the corpus luteum." This figure has been reproduced by kind permission of Dr. C. G. Hartman, from his paper "The Homology of Menstruation" (1929 *c*). It may be noted that while Hartman records in this chart that "Hyperæmia and Hemorrhage" occur at the time of ovulation, he does *not* indicate any endometrial degeneration occurring at this time. It is usually stated, however, that endometrial degeneration *does* occur at the time of ovulation (see, for instance, Corner's remarks on this point, p. 739 above).

Hartman has offered an interpretation of the menstrual cycle (1929 *c*) which depends upon the occurrence of interval uterine bleeding. "Ovulation takes place almost exactly in the middle of the menstrual cycle, counting from the first appearance of the menstrual flow. Under the influence of the expanding Graafian follicles, growth of the endometrium is initiated and congestion produced, resulting in slight extravasations of blood into the mucosal stroma and probably diapedesis into the uterine cavity. After ovulation, under the influence of the corpus luteum, the premenstrual growth and swelling of the endometrium take place. In

the absence of fertilization of the ovum, and on the consequent degeneration of the corpus luteum, the hypertrophied functionalis desquamates and the menstrual hemorrhage results." Upon this view the menstrual cycle is directly homologous with the phases of the œstrous cycle of the bitch (see Diagram 2)—the "inter-menstrual bleeding" being the "homologue of pro-œstrum in the dog".

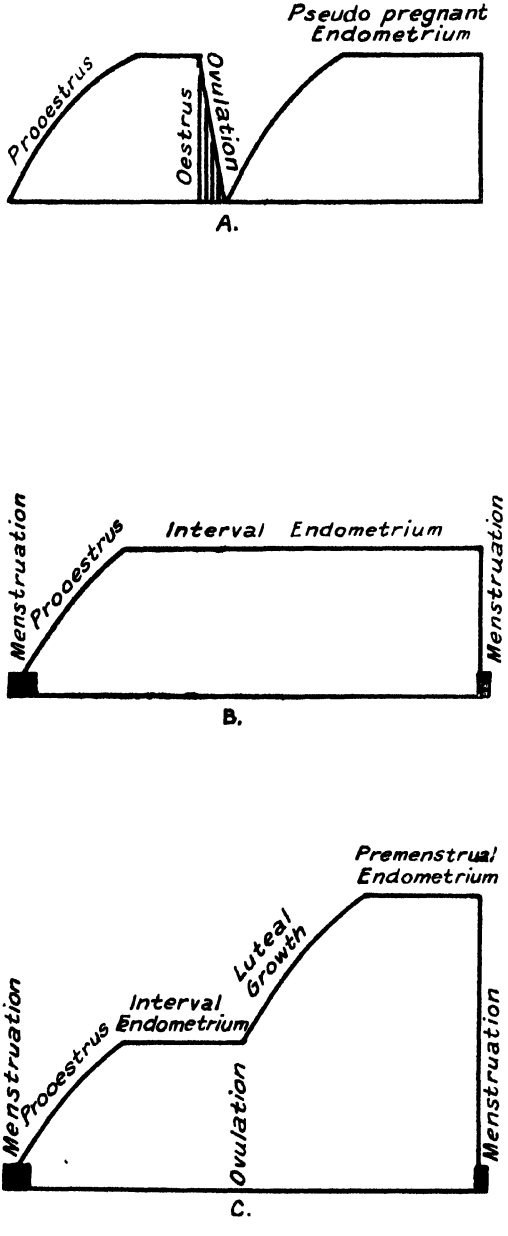
There are, however, objections to this interpretation. As already pointed out (p. 741), the fact that interval bleeding does not appear to be of ovarian origin does not necessarily prove that it is uterine. A serious objection to the view that it is uterine is the fact that histological studies of the endometrial changes of both women and monkeys have failed to reveal any uterine bleeding or degeneration occurring at any time other than at the true menstrual periods. Corner particularly notes that the endometrium of a monkey which has just ovulated showed none of the degenerative signs that mark œstrus in the lower mammal (see p. 739). Apart, however, from this conflicting evidence, Hartman's interpretation of the menstrual cycle in no way explains menstruation when ovulation has not occurred, *i.e.* menstruation at the proper cyclical period from an interval endometrium. Moreover, on p. 706, I noted a cycle in a Pig-tailed Macaque in which menstruation occurred at its expected time in spite of the persistence of swelling in the animal's sexual skin. This evidence of the maintenance of follicular changes throughout the cycle directly conflicts with Hartman's suggestion that the follicular phase ends with endometrial bleeding in the middle of the cycle. The origin and significance of the interval erythrocytes found by him have yet to be explained.

In 1929 I suggested an interpretation of the primate menstrual cycle which seems to be in closer agreement with the established facts than are any of the theories discussed above. According to this interpretation, menstruation in cycles in which ovulation occurs represents a delayed breakdown of the pro-œstrous growth which heralds ovulation, combined with the breakdown of the pseudo-pregnant growth which follows the *same* ovulation (see Diagram 3 C). In cycles in which ovulation does not occur menstruation represents only the delayed degeneration of the pro-œstrous endometrium (see Diagram 3 B).

Certain facts are especially significant.

It has been noted above that sexual skin changes in the sub-human primate are controlled by the follicular hormone, œstrin. Moreover, the regeneration of the endometrium following menstruation and its transition to the "interval" type of endometrium is comparable to the pro-œstrous growth which occurs in the lower mammal. It is clear, however, that neither the sexual skin changes nor the uterine cycle are directly dependent upon the morphological ovarian cycle, viz. the maturation and rupture of follicles: for in those cycles in which ovulation does not occur, signs of sexual skin activity nevertheless disappear about the middle of the cycle, and this is followed, after an interval of approximately fourteen days, by a normal menstruation from an interval endometrium. There is evidence, too, that the follicular hormone is active throughout the entire cycle. In the Pig-tailed Macaque, noted on p. 706, the action of œstrin was evidenced throughout an entire cycle in the activity of the sexual skin: yet this cycle was normal as judged by the time of menstruation. Moreover, a cycle in which no ovulation occurs consists of a follicular phase only, as no corpus luteum is developed: yet the pro œstrous endometrium does not immediately degenerate after the apparent withdrawal of the œstrous stimulus (as judged by the sexual skin changes) at about the middle of the cycle. It persists as an interval endometrium for about two weeks, until menstruation occurs at the same time as in cycles with ovulation. Now it is known that in lower mammals different amounts of œstrin are necessary to produce œstrous changes in different parts of the generative tract—far less œstrin is necessary, for instance, to produce cornification in the mouse vagina than is necessary to produce pro-œstrous changes in the mouse uterus (see Parkes, 1929). A similar difference in the effects of œstrin on different parts of the generative

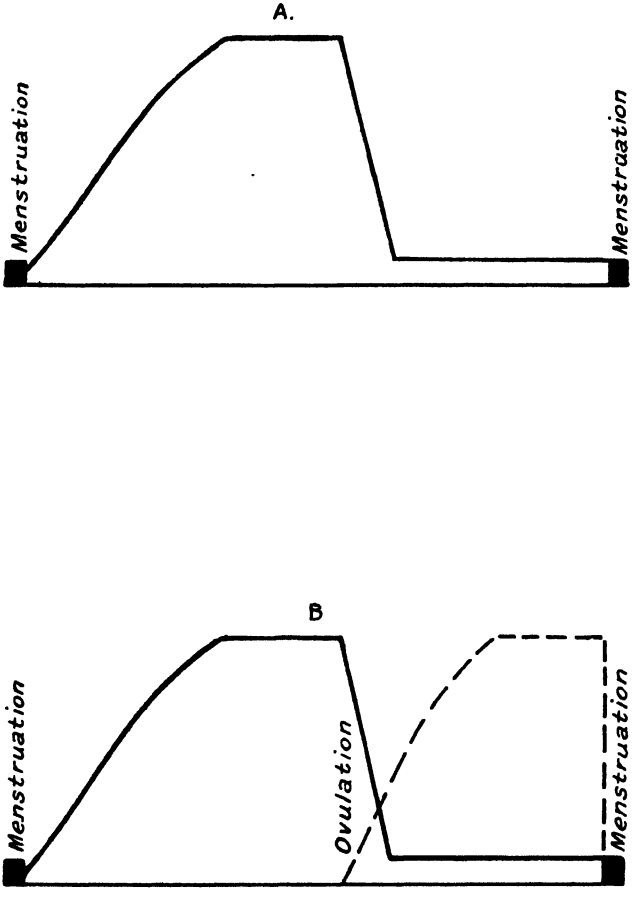
Diagram 3.



Diagrammatic representation of the endometrial changes in the œstrous cycle of A, the dog: B, the primate (cycle without ovulation): C, the primate (cycle with ovulation).

tract probably occurs also in the Primates. The independent variation of the coloration and the swelling of the sexual skin of *M. mulatta* is almost certainly due to variation in the amount of œstrin secreted (pp. 722, 737). It is conceivable, therefore, that different amounts of œstrin are required to cause sexual skin activity on the one hand and uterine changes on the other. One cycle of the Pig-tailed Macaque, noted on p. 706, strongly suggests this. Her sexual skin

Diagram 4.



Diagrammatic representations of the phases of the primate menstrual cycle. Unbroken line: the variation in the effects of the follicular hormone. Broken line: the variation in the effects of the corpus luteum. A. Cycle in which ovulation does not occur. B. Cycle in which ovulation occurs.

remained almost quiescent throughout an entire cycle: yet uterine changes had evidently taken place, for she menstruated at the normal time.

The sequence of events in the primate menstrual cycle appears, therefore, to be as follows:—

Œstrin is secreted in increasing quantity throughout the earlier half of the

cycle (see p. 722). It produces changes in the sexual skin, growth in the endometrium (not exceeding the amount characteristic of the "interval" stage), and growth in the mammary glands. At about the middle of the cycle the amount secreted abruptly diminishes. Sexual skin changes disappear, but it would seem that sufficient hormone remains operative to maintain the interval endometrium unchanged for a further two weeks, until the cycle ends with menstruation. The post-menstrual growth of the endometrium and its transition to the "interval" stage is thus comparable to the pro-œstrous growth which occurs in the lower mammal. If ovulation does not occur, no further growth takes place in the endometrium after the middle of the cycle: the animal menstruates a fortnight later from an "interval" endometrium which has been produced, and presumably maintained, by the follicular hormone. When ovulation occurs (at about the middle of the cycle) the subsequent development of a corpus luteum determines a further growth-phase, which is superimposed on the follicular "interval" endometrium. The uterine mucous membrane now becomes "premenstrual" in type. If conception has not occurred, the corpus luteum retrogresses about fourteen days after ovulation, and the "premenstrual" endometrium breaks down. In the ovulating non-pregnant female primate, therefore, menstruation represents both pseudo-pregnant destruction and a *delayed* pro-œstrous degeneration.

According to this view, the main difference between the menstrual cycle of the primate and the œstrous cycle of the lower mammal lies in the distribution of their respective follicular phases. It is generally believed that in the bitch, for instance, the follicular phase ends abruptly with pro-œstrous destruction, and that it does not extend into the ensuing luteal phase (see lowest section of Diagram 2) The pseudo-pregnant endometrium is built up, under the influence of luteal hormones, from an endometrium that has undergone degeneration as a result of the removal of the stimulus of the follicular hormone at ovulation. On the other hand, the follicular phase of the primate cycle, though its main effects occur in the earlier half, is prolonged over the entire cycle, and pseudo-pregnant growth is *superimposed upon* a persisting pro-œstrous endometrium (see Diagram 3 B and C, and Diagram 4).

If this interpretation be correct, the differences in sexual behaviour between the Primates and the lower mammals are only reflections of their different sexual physiological mechanisms. The matings of the lower mammal are confined to short periods circumscribed by activity of the follicular hormone. The matings of the primate are diffused over the entire cycle, paralleling the continued action of the follicular hormone, but varying in frequency according to the varying degrees of activity of that hormone.

Summary.

(1) No definite statement can as yet be made about the breeding habits of any sub-human primate. New World monkeys are said to breed during special seasons. Certain Old World monkeys are said to be fertile in their natural habitat at all times of the year. Other Old World monkeys, on the other hand, are said to give birth during only one period of the year, though it is known that the non-pregnant female experiences an uninterrupted series of menstrual cycles throughout the year. It is believed that these monkeys ovulate only during limited seasons.

(2) All female Old World primates experience approximately four-weekly menstrual cycles. Many of them manifest cyclical changes, varying in degree, in the colour and form of the external pudendal organs and the skin adjacent to them, an area known as "the sexual skin." These changes are shown, for instance, by the Chimpanzee, Orang, *Cercopithecus talapoin*, all the species of the genus *Cercocebus*, most of the species of the genus *Macaca*, and all the species of the genera *Papio* and *Mandrillus*. The sexual skin becomes active immediately after the

onset of menstruation, and reaches its maximum of activity before the middle of the cycle. Shortly after the middle of the cycle the sexual skin suddenly resumes its quiescent appearance, in which condition it remains until the onset of the next catamenia, when it again becomes active.

So far as is known, New World monkeys do not undergo menstrual cycles.

(3) The causation of the cyclical change in the sexual skin of *M. mulatta* has been investigated mainly by Allen, who has shown that activity of the sexual skin is dependent upon activity of the follicular hormone, œstrin. The natural cyclical activity of the sexual skin of *M. mulatta* is the result of the stimulus of the follicular hormone, which becomes operative at the beginning of the menstrual cycle, with the beginning of follicular growth, and which ceases usually about the middle of the cycle. Ovulation, when it occurs, happens about the middle of the cycle. A similar relationship between sexual skin activity and the time of ovulation exists in *P. porcarius*. Activity of the sexual skin is thus part of the follicular phase of the menstrual cycle.

(4) Primates that show marked cyclical changes in the sexual skin are more active sexually than those that do not. Monkeys that copulate in captivity do so at all times, but copulation occurs most frequently during the period of maximum sexual skin activity. Ovulation occurs, if at all, about the end of this period. The "heat" period of the primate, therefore, has the same biological significance as the "œstrus" of the lower mammal, *i.e.* mating occurs most frequently when it is likely to be fertile.

(5) Puberty in monkeys begins with activity of the sexual skin. The sexual skin remains active for about a month and then resumes its inactive appearance. Menstruation follows soon after it has become inactive. Sub-human primates become sexually mature soon after the permanent incisors have erupted, that is, at a stage of growth corresponding approximately to a girl of seven or eight. Pregnancy has been reported in a chimpanzee whose permanent canines had not erupted, *i.e.* when the chimpanzee was about ten years old.

(6) Pregnancy in the chimpanzee is said to last nine months. The duration of gestation in the rhesus macaque is said to be from 149 to 174 days, the average being 164·3 days. In the Hamadryas baboon pregnancy lasts from 154 to 189 days, the average duration being 169 days.

Swelling of the sexual skin does not occur during either pregnancy or lactation in the baboon, pig-tailed macaque, and chimpanzee. On the other hand, the sexual skin of the pregnant and lactating rhesus macaque is highly coloured. Under relatively natural circumstances the usual absence of sexual skin changes is reflected in behaviour, for pregnant and lactating monkeys seldom copulate.

(7) Ovulation in the monkey occurs about midway between two menstrual periods. Monkeys, however, do not ovulate every cycle.

(8) After menstruation the destroyed endometrium is regenerated, and by the middle of the cycle is of the "interval" type. The endometrium is low and the glands are short and straight. If ovulation does not then occur, the endometrium remains in this condition for about another two weeks and then breaks down. Menstruation in cycles without ovulation therefore takes place from an "interval" endometrium. If ovulation occurs, the subsequent development of a corpus luteum is paralleled by further growth in the endometrium, which becomes "premenstrual" in type. The endometrium is spongy and deep: the blood-supply is increased; the glands are tortuous and the basal glands are increased; the surface and glandular epithelium is high. If the ovum is not fertilized, the "premenstrual" endometrium breaks down about two weeks after ovulation. Menstruation in cycles with ovulation therefore takes place from a "premenstrual" endometrium.

(9) The rhesus macaque, the Anubis and Yellow baboon, and the Abyssinian cercopitheque show the same cyclical vaginal changes. Leucocytes are usually

absent from a vaginal smear about the middle of the cycle, and most numerous immediately before, during, and after menstruation. Epithelial desquamation is greatest about the middle of the cycle.

(10) The follicular phase of the primate menstrual cycle, though its main effects occur in the earlier half, as in the œstrous cycle of the lower mammal, is prolonged over the entire cycle. Cycles without ovulation consist of only a follicular phase. When ovulation occurs, a luteal phase is superimposed upon the latter half of the follicular phase. In the lower mammal (*e. g.*, bitch) the pseudo-pregnant endometrium is built up under the influence of luteal hormones from an endometrium that has undergone degeneration as a result of the removal of the stimulus of the follicular hormone at ovulation. In the primate, on the other hand, pseudo-pregnant growth is superimposed upon a pro-œstrous endometrium.

It is here suggested that in the ovulating non-pregnant female primate, menstruation represents both pseudo-pregnant destruction and a *delayed* pro-œstrous degeneration. In the absence of ovulation, menstruation represents only *delayed* pro-œstrous degeneration.

I wish to acknowledge the stimulating interest shown in this work by Prof. G. Elliot Smith, F.R.S., and Prof. J. P. Hill, F.R.S, of the Institute of Anatomy, University College, London, and by Sir Peter Chalmers Mitchell, F.R.S., Secretary of the Zoological Society of London; the generous co-operation of Dr. A. S. Parkes, of University College, London, to whom I am also indebted for permission to use the data on p. 720; the assistance of Dr. G. M. Vevers, Superintendent of the Gardens of the Zoological Society of London, in facilitating the routine observation of monkeys; and the help of keepers in the Zoological Gardens, particularly that of Keepers A. S. Budd and C. Harwood. Other acknowledgments have been included in the text.

Bibliography.

Allen, Edgar. 1926 *a*. Progress of Work on the Mechanism of the Menstrual Cycle of the Monkey, *Macacus rhesus*. Anat. Rec., Philadelphia, vol. xxxii. p. 226 (Abstract).

——— 1926 *b*. The Time of Ovulation in the Menstrual Cycle of the Monkey, *Macacus rhesus*. Proc. Soc. Exper. Biol. & Med., New York, vol. xxiii. pp. 381–383.

——— 1926 *c*. The Menstrual Cycle in the Monkey: Effect of Double Ovariectomy and Injury to Large Follicles. Proc. Soc. Exper. Biol. & Med., New York, vol. xxiii. pp. 434–436.

——— 1927. The Menstrual Cycle of the Monkey, *Macacus rhesus*: Observations on Normal Animals, the Effects of Removal of the Ovaries and the Effects of Injections of Ovarian and Placental Extracts into the Spayed Animals. Contribution to Embryol., Washington, 98, vol. xix. pp. 1–44.

——— 1928 *a*. Effects of Ovariectomy upon Menstruation in Monkeys. Amer. Journ. Physiol., Baltimore, vol. lxxxv. pp. 471–475.

——— 1928 *b*. Sex Characteristics in Monkeys. Proc. Soc. Exp. Biol. & Med., New York, vol. xxv. pp. 325–327.

——— 1928 *c*. An Unfertilized Tubal Ovum from *Macacus rhesus*. Anat. Rec., Philadelphia, vol. xxxvii. pp. 351–356.

——— 1928 *d*. Further Experiments with an Ovarian Hormone in the Ovariectomized adult Monkey, *Macacus rhesus*, especially the Degenerative Phase of the Experimental Menstrual Cycle. Amer. Journ. Anat., Philadelphia, vol. xlii. pp. 467–486.

——— 1928 *e*. Reactions of Immature Monkeys (*Macacus rhesus*) to Injections of Ovarian Hormone. Journ. Morph. & Physiol., Boston, vol. xlvi. pp. 479–495.

——— Pratt, J. P., & Doisy, E. A. 1925. The Ovarian Follicular Hormone: its Distribution in Human Genital Tissues. Journ. Amer. Med. Assoc., Chicago, vol. lxxxv. pp. 399–404.

Allesch, G. J. von. 1921. Geburt und erst Lebensmonate eines Schimpansen. Naturwissenschaften, Berlin, vol. ix. pp. 774–776.

Anderson, J. 1878. Anatomical and Zoological Researches in Western Yunnan. Vol. i. Quaritch, London.

BINGHAM, HAROLD C. 1928. Sex Development in Apes. Comp. Psych. Monographs, Baltimore, vol. v. pp. 1–165.

BLANFORD, W. T. 1888–1891. The Fauna of British India.—Mammalia. Taylor & Francis, London.

BRESCHET, G. 1845. Recherches Anatomiques et Physiologiques sur la Gestation des Quadrumanes. Mem. Acad. Sci. Paris, tome xix.

BRIFFAULT, R. 1927. The Mothers. Vol. i. Allen & Unwin, London.

BUFFON, COMTE DE. 1775. Natural History. Translated by W. Kendrick and J. Murdoch. Vol. iv. T. Bell, London.

BURTON, R. F. 1876. Two Trips to Gorilla Land and the Cataracts of the Congo. London.

COLLINGS, M. R. 1926. A Study of the Cutaneous Reddening and Swelling about the Genitalia of the Monkey. *M. rhesus*. Anat. Rec., Philadelphia, vol. xxxiii. pp. 271–278.

CORNER, G. W. 1923 *a*. Œstrus, Ovulation, and Menstruation. Physiol. Review, Baltimore, vol. iii. pp. 457 482.

——— 1923 *b*. Ovulation and Menstruation in *Macacus rhesus*. Contrib. to Embryol. no. 15, Carnegie Inst. of Washington, pp. 73–101.

——— 1927. The Relation between Menstruation and Ovulation in the Monkey. Journ. Amer. Med. Assoc., Chicago, vol. lxxxix. pp. 1838–1840.

CUVIER, G. 1834. The Animal Kingdom. Vol. i. G. Henderson, London.

DARWIN, C. 1871. The Descent of Man. 1901 Edition. John Murray, London.

——— 1876. Sexual Selection in relation to Monkeys. Nature, London, vol. xv. p. 18.

DISTANT, W. L. 1897. Notes on the Chacma Baboon. Zoologist, London (4), vol. i. pp. 29–32.

EHLERS, E. 1881. Beitrage zur Kenntnis des Gorilla und Chimpanse. Abh. Phys. Cl. Ges. Wiss. Gottingen, Bd. xxviii. pp. 3–77.

FEE, A. R. & PARKES, A. S. 1929. Studies on Ovulation. 1. The Relation of the Anterior Pituitary Body to Ovulation in the Rabbit. Journ. Physiol., London, vol. lxvii. pp. 383 388.

FISCHER, J. VON. 1876. Aus dem Leben eines jungen Mandril (*Cynocephalus mormon*). Der Zoolog. Garten, Frankfurt, Jahr. xvii. pp. 116–133.

FITZSIMONS, F. W. 1919. The Natural History of South Africa. Vol. i. Mammals. Longmans Green, London.

FLOWER, S. S. 1929. Vertebrate List. Vol. i. Mammals. Zoological Society, London.

FORBES, H O. 1894. Handbook to the Primates. Allen, London.

FOX, H. 1929. The Birth of Two Anthropoid Apes. Journ. Mamm. Baltimore, vol. x. pp. 37–51.

FRIEDENTHAL, H. 1908. Beitrage zur Naturgeschichte des Menschen.—Lieferung 1. Das Wollhaarkleid des Menschen. Fischer, Jena.

GEAR, H. S. 1926. The Œstrous Cycle of the Baboon. S. A. Journ. Sci., Capetown, vol. xxiii. pp. 706–712.

H., C. 1880. Sketches of Natural History at Gibraltar. The Field, London, p. 79.

HAAN, J. A. BIERENS DE. 1925. Experiments on Vision in Monkeys. I. The Colour-sense of the Pig-tailed Macaque (*Nemestrinus nemestrinus* L.). Journ. Comp. Psychol., Baltimore, vol. v. pp. 417–453.

HAMILTON, G. V. 1914. A Study of Sexual Tendencies in Monkeys and Baboons. Journ. Anim. Behav., Boston, vol. iv. pp. 295–318.

HAMMOND, J. 1925. Reproduction in the Rabbit. Oliver & Boyd, London.

HARTMAN, C. 1927. Menstruation without Ovulation in *Macacus rhesus*. Anat. Rec., Philadelphia, vol. xxxv. p. 13 (Abstract).

——— 1928 *a*. Menstruation in *Macacus rhesus* with Interval Endometrium. Anat. Rec., Philadelphia, vol. xxxviii. p. 47 (Abstract).

——— 1928 *b*. The Period of Gestation in the Monkey, *Macacus rhesus*. Science, New York. n. s. vol. lxvii. p. 15.

——— 1928 *c*. Description of Parturition in *Macacus rhesus*, together with Data on the Gestation Period and the Phenomena incident to Pregnancy and Labor. Bull. Johns Hopkins Hospital, Baltimore, vol. xliii. pp. 33–51.

——— 1928 *d*. Gestation in a Monkey (*Macacus rhesus*) and Associated Phenomena. Amer. Journ. Obst. & Gyn., New York, vol. xv. pp. 534–540.

——— 1928 *e*. The Period of Gestation in the Monkey (*Macacus rhesus*): First Description of Parturition in Monkeys, Size and Behavior of the Young. Journ. Mamm., Baltimore, vol. ix. pp. 181–194.

HARTMAN, C. 1928*f*. A readily detectable Sign of Ovulation in the Monkey. Science, New York, vol. lxviii. no. 1767, pp. 452–453.

——— 1929*a*. Three Types of Uterine Bleeding in the Monkey and the Homology of Menstruation. Anat. Rec., Philadephia, vol. xlii. p. 61 (Abstract).

——— 1929*b*. Uterine Bleeding as an Early Sign of Pregnancy in the Monkey (*Macacus rhesus*), together with Observations on the Fertile Period of the Menstrual Cycle. Bull. Johns Hopkins Hospital, Baltimore, vol. xliv. pp. 155–164.

——— 1929*c*. The Homology of Menstruation. Journ. Amer. Med. Assoc., Chicago, vol. xcii. pp. 1992–1995.

——— 1929*d*. The Period of Gestation in the Monkey, *Macacus rhesus*. Anat. Rec., Philadelphia, vol. xliv. p. 226 (Abstract).

——— 1929*e*. A Breeding and a Non-Breeding Season in the Monkey, *Macacus rhesus*. Anat. Rec., Philadelphia, vol. xliv. p. 226 (Abstract).

——— 1929*f*. The Fertile Period of the Menstrual Cycle in the Monkey. Anat. Rec., Philadelphia, vol. xliv. p. 226 (Abstract).

HEAPE, W. 1894. The Menstruation of *Semnopithecus entellus*. Phil. Trans. Roy. Soc. London, vol. clxxxv. B, pp. 411 471.

——— 1896. The Menstruation and Ovulation of *Macacus rhesus*. Proc. Roy. Soc. London, vol. lx. pp. 202–205.

——— 1898. The Menstruation and Ovulation of Monkeys and the Human Female. Trans. Obst. Soc., London, vol. xl. pp. 161–174.

——— 1900. The "Sexual Season" of Mammals and the Relation of the "Pro-œstrum" to Menstruation. Quart. Journ. Micros. Sci., London, vol. xliv. pp. 1–70.

HINGSTON, R. W. G. 1920. A Naturalist in Himalaya. Witherby, London.

HOFSCHLÄGER, R. 1925. Geschlecht und Gesellschaft in der Zeit der Menschwerdung. Geschlecht und Gesellsch. ft. Dresden, vol. xiii. pp. 1 34.

HUXLEY, T. H. 1863. Man's Place in Nature. Everyman's Library Edition: Dent, London, 1921.

KEITH, A. 1899. On the Chimpanzees and their Relationship to the Gorilla. Proc. Zool. Soc. London, pp. 296–312.

KEMPF, EDWARD J. 1917. The Social and Sexual Behaviour of Infra-human Primates, with some Comparable Facts in Human Behavior. Psychoanalytic. Rev., New York, vol. iv. pp. 127–154.

KÖHLER, W. 1927. The Mentality of Apes. Translated from the Second Revised Edition by Ella Winter, B.Sc. Kegan Paul, Trench, Trubner & Co., Ltd., London.

LANGLEY, J. N. 1890. The Innervation of the Pelvic Viscera. Proc. Physiol. Soc. London, vol. xii. no. 6, pp. xxiii–xxvi.

——— & SHERRINGTON, C. S. 1891. On Pilo-motor Nerves. Journ. Physiol., London, vol. xii. pp. 278–291.

LOVERIDGE, A. 1923. Notes on East African Mammals. Proc. Zool. Soc. London, pp. 685–739.

LUCAS, N. S., HUME, M., & SMITH, H. H. 1927. On the Breeding of the Common Marmoset (*Hapale jacchus* Linn.) in Captivity when irradiated with Ultra-violet Rays. Proc. Zool. Soc London, pp. 447–451.

MALINOWSKI, B. 1927. Sex and Repression in Savage Society. Kegan Paul, Trench, Trubner & Co., Ltd., London.

MARSHALL, F. 1922. The Physiology of Reproduction. Longmans Green, London. 2nd Edition.

——— 1927. On the Pro-œstrum and Pseudo-Pregnancy. Quart. Journ. Exper. Physiol., London, vol. xvii. pp. 205 210.

——— & JOLLY, W. 1905. Contributions to the Physiology of Mammalian Reproduction. Part I. The Œstrous Cycle in the Dog. Phil. Trans. Roy. Soc., London, B. vol. cxcviii. pp. 99–122.

——— & HALNAN, E. T. 1917. On the Post-œstrous Changes occurring in the Generative Organs and Mammary Glands of the Non-Pregnant Dog. Proc. Roy. Soc. London, B, vol. lxxxix. pp. 546–559.

MILLER, GERRIT S. 1928. Some Elements of Sexual Behavior in Primates, and their Possible Influence on the Beginnings of Human Social Development. Journ. Mammalogy, Baltimore, vol. ix. pp. 273–293.

MONTANÉ, L. 1928. Histoire d'une famille de Chimpanzés. Bull. et Mem. Soc. Anthrop., Paris.

MURIE, J. 1872. Observations on the Macaques. III. The Formosan or Round-Faced Monkey. Proc. Zool. Soc. London, pp. 772–774.

PAPANICOLAOU, G. N. S. 1926. A Specific Inhibitory Hormone of the Corpus luteum. Journ. Amer. Med. Assoc., Chicago, vol. lxxxvi. pp. 1422–1424.

PARKES, A. S. 1929. The Internal Secretions of the Ovary. Longmans Green, London.

——— & BRAMBELL, F. W. R. 1928. The Causation of the Anœstrous Period. Journ. Physiol., London, vol. lxiv. no. 4, pp. 388–392.

PERCY, Professor. 1844. On the Management of various Species of Monkeys in Confinement. Proc. Zool. Soc. London, p. 82.

POCOCK, R. I. 1905. Observations upon a Female Specimen of the Hainan Gibbon (*Hylobates hainanus*) now living in the Society's Gardens. Proc. Zool. Soc. London, vol. ii. pp. 169–180.

——— 1906. Notes upon Menstruation, Gestation, and Parturition of some Monkeys that have lived in the Society's Gardens. Proc. Zool. Soc. London, vol. ii. pp. 558–570.

——— 1925. The External Characters of the Catarrhine Monkeys and Apes. Proc. Zool. Soc. London, pp. 1479–1579.

READE, W. WINWOOD. 1864. Savage Africa. Smith Elder, London.

RENGGER, J. R. 1830. Naturgeschichte der Saugethiere von Paraguay. Basel.

RIDLEY, H. N. 1895. The Mammals of the Malay Peninsula. Nat. Sci., London, vol. vi. pp. 23–29.

ROBERTSON, D. D. 1929. Effects induced in Ovariectomised Monkeys by Injections of Extracts of Ovaries and Implants of corpora lutea. Anat. Rec., Philadelphia, vol. xlii. p. 61 (Abstract).

SAVAGE, T. S., & WYMAN, J. 1844. Observations on the External Characters and Habits of the *Troglodytes niger*, and on its Organization. Bost. Journ. of Nat. Hist., vol. iv. pp. 377–386.

SCLATER, P. L. 1864. Notes on the Quadrumana living in the Society's Menagerie. Proc. Zool. Soc. London, pp. 710–711.

——— 1900. On the *Macacus inuus* of Gibraltar. Proc. Zool. Soc. London, p. 773.

SHARPE, NEVILLE A. DYCE. 1927. Notes on the Gorilla. Proc. Zool. Soc. London, p. 1006.

SHAW, W. 1925. The Relation of Ovarian Function to Menstruation. Journ. Phys., London, vol. lx. pp. 193–207.

SHERRINGTON, C. S. 1892. Notes on the Arrangement of some Motor Fibres in the Lumbo-sacral Plexus. Journ. Physiol., London, vol. xiii. pp. 621–772.

——— 1892. Experiments in Examination of the Peripheral Distribution of the Fibres of the Posterior Roots of some Spinal Nerves. Proc. Roy. Soc., London, vol. lii. pp. 333–337.

SOKOLOWSKY, ALEXANDER. 1923. The Sexual Life of the Anthropoid Apes. Urologic and Cutaneous Review, St. Louis, vol. xxvii. pp. 612–615.

STEVENSON-HAMILTON, J. 1912. Animal Life in Africa. William Heinemann, London.

SUTTON, B. J. 1880. Menstruation in Monkeys. Brit. Gynæ. Journ., London, vol. ii.

TICKELL, S. R. 1864. Note on the Gibbon (*Hylobates lar*) of Tenasserim. Journ. Asiat. Soc. Bengal, Calcutta, vol. xxxiii. pp. 196–199.

VAN HERWERDEN, M. 1906. Beitrag zur Kentniss des menstruellen Cyklus. Monatsschr. f. Geburtschulfe und Gynak, Berlin, vol. xxiv. pp. 730–748.

WATSON, J. B. 1909. Some Experiments bearing upon Color-vision in Monkeys. Journ. Comp. Neurol. & Psychol., Philadelphia, Pa., vol. xix. pp. 1–28.

WESTERMARCK, E. 1921. The History of Human Marriage. 5th Edition. Macmillan, London.

WISLOCKI, G. B., & HARTMAN, C. 1929. On the Placentation of a Macaque (*Macacus rhesus*), with Observations on the Origin of the Blood constituting the Placental Sign. Bull. Johns Hopkins Hospital, Baltimore, vol. xliv. no. 3, pp. 165–185.

YERKES, R. M. 1928. The Mind of a Gorilla. Part 3. Memory. Comp. Psych. Monog., Baltimore, vol. v. no. 2, pp. 1–92.

——— & YERKES, A. W. 1929. The Great Apes. A Study of Anthropoid Life. Yale Univ. Press, New Haven.

ZUCKERMAN, S. 1928. Age-changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimation of Age; with a Note on the Taungs Ape. Proc. Zool. Soc. London, pp. 1–42.

——— 1929. The Social Life of the Primates. Realist, Macmillan, London, vol. i. no. 4, pp. 72–88.

Explanation of the Charts.

Chart 1 and Charts 3 to 14 are diagrammatic representations of the "menstrual histories" of thirteen monkeys over a period of almost a year. The curves indicate the degree of activity of the sexual skin. Chart 2 (p. 704) is a growth curve of a *Macaca mulatta* (=*Macacus rhesus*).

Chart 1 (p. 701). The menstrual cycles of a *Cercocebus albigena*. The days in which vaginal bleeding was observed are indicated in black along the base-line.

Chart 3 (p. 707). The "menstrual history" of a *Macaca nemestrina*. Only the first day of each period of bleeding is indicated on the base-line.

Charts 4–12 (pp. 712–713). The "menstrual histories" of nine Hamadryas Baboons, *Papio hamadryas*. Only the first day of each period of bleeding is indicated on the base-line. In all cycles swelling of the sexual skin has been indicated, for the sake of uniformity, as beginning on the second day of the cycle. As explained in the text (see p. 711), swelling becomes noticable as a rule any time between the first and fourth days of the cycle. Those parts of charts 6, 10, and 14 drawn in "broken-line" represent periods when observations were not made. The curves for these periods have been constructed according to the general plan of the observed cycles.

Chart 13 (p. 715). The menstrual cycles of a *Papio anubis*. Explanation otherwise as in Charts 4–12.

Chart 14 (p. 716). The menstrual cycles of a *Papio cynocephalus*. Explanation otherwise as in Charts 4–12.

[More cycles are indicated in these charts than are considered in the text.]

EXPLANATION OF THE PLATES.

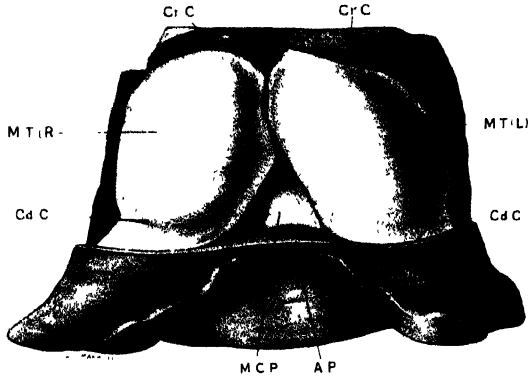
Plate I.

Longitudinal section of the body and part of the cervix of the uterus of *Macaca radiata*, showing the nature of the cervical mucous membrane.

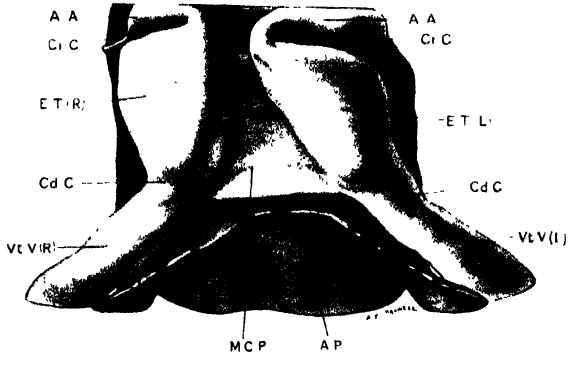
Plate II.

Section of left ovary of *Papio hamadryas* (C. 12), showing a recently ruptured follicle. The central cavity is filled with a coagulum.

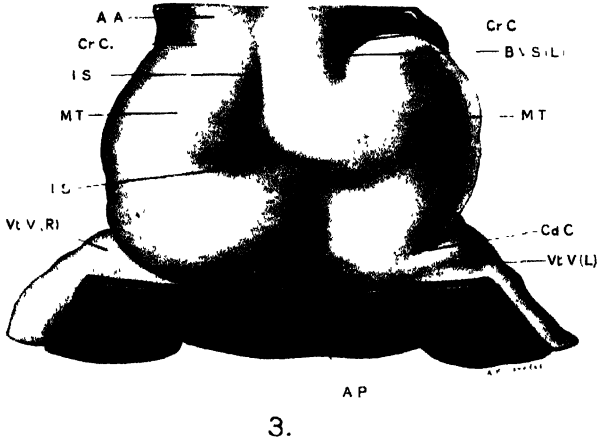
Photomicrographs by Mr. F. J. Pittock.



1.

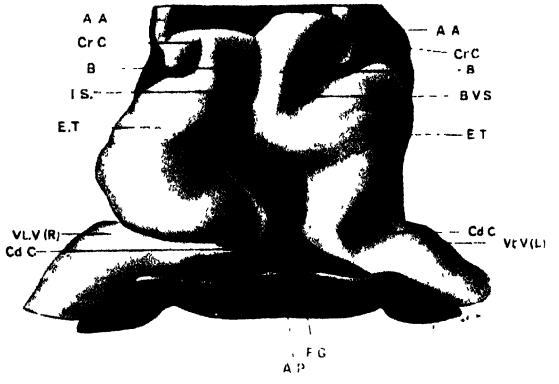


2.

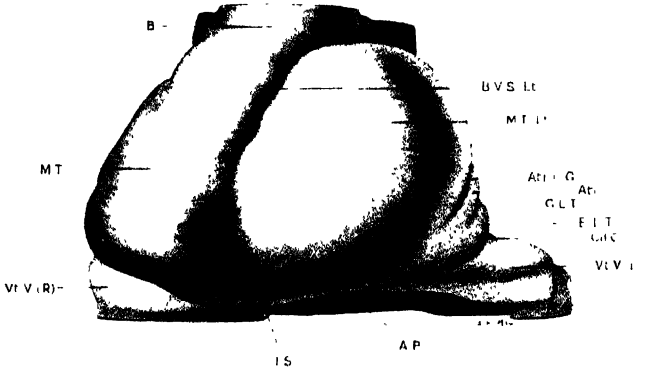


3.

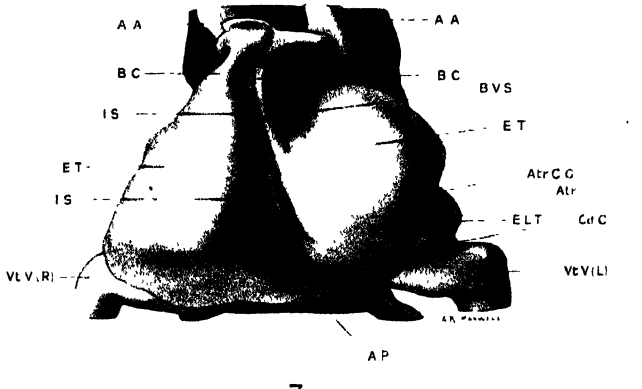
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



4.



5

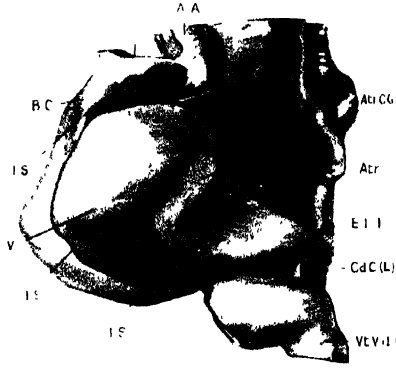


7.

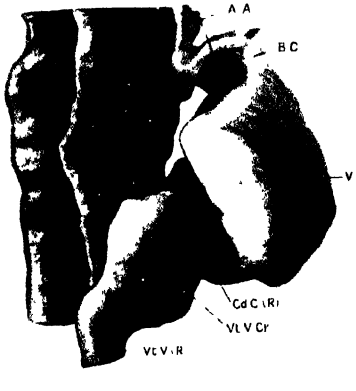
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



6.

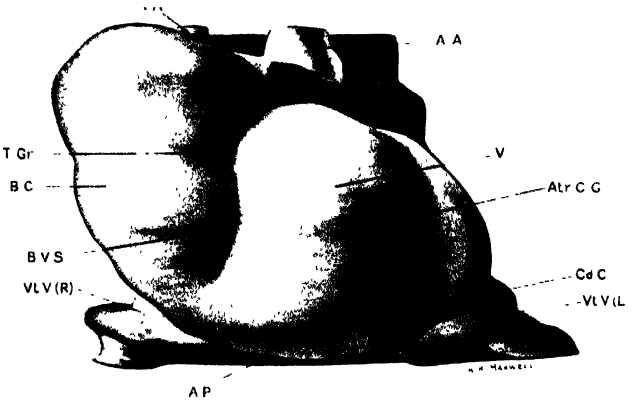


8.

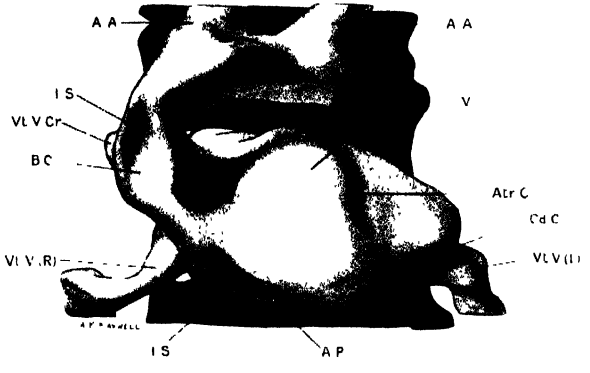


9.

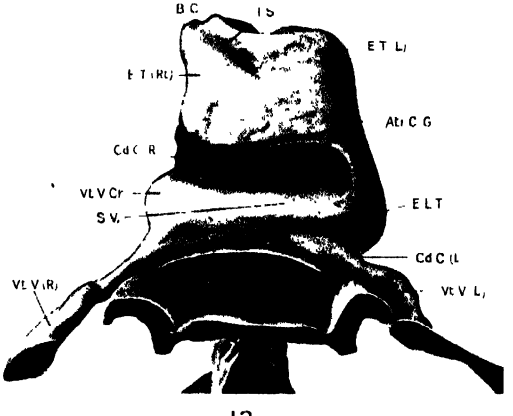
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



10.

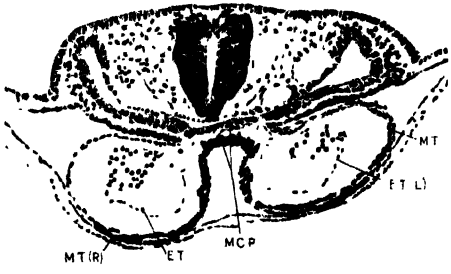


11.

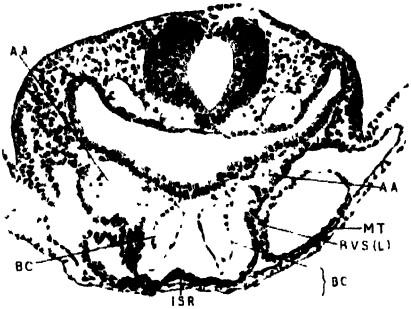


13.

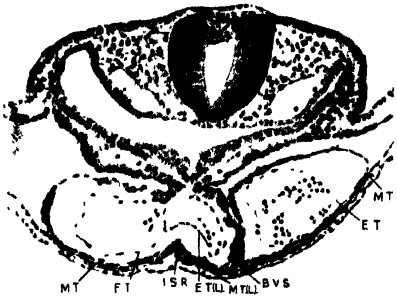
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



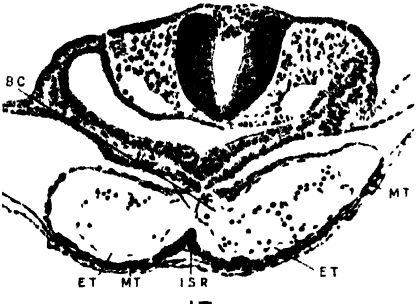
14



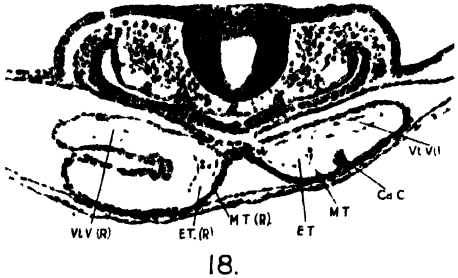
15



16.

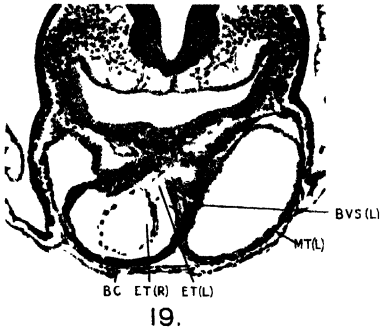


17.

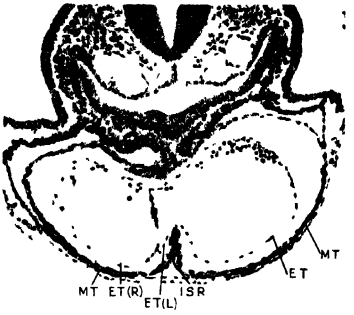


18.

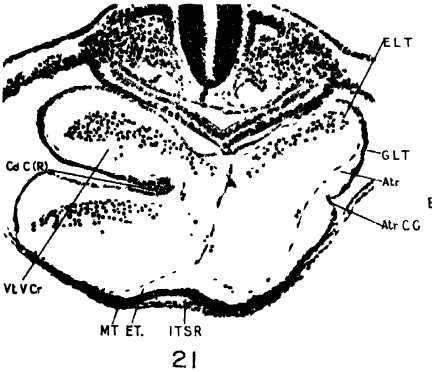
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



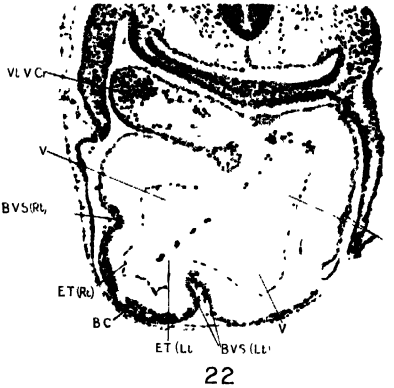
19.



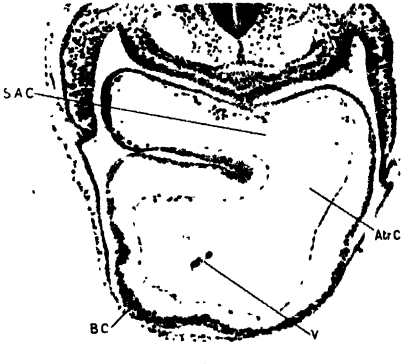
20.



21

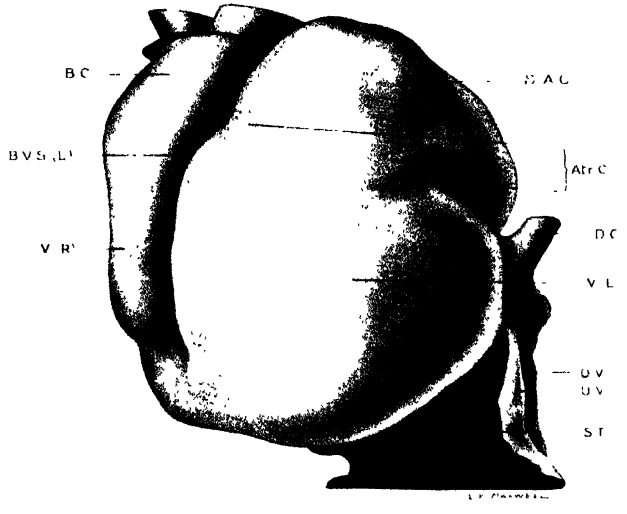


22

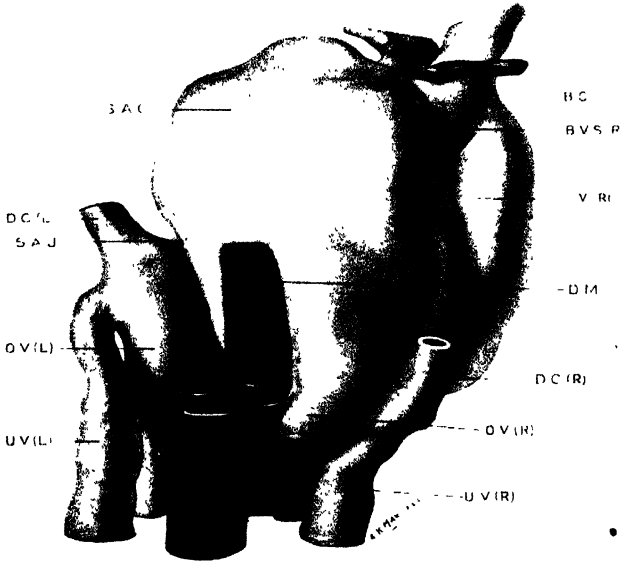


23.

THE DEVELOPMENT OF THE HEART IN THE RABBIT.

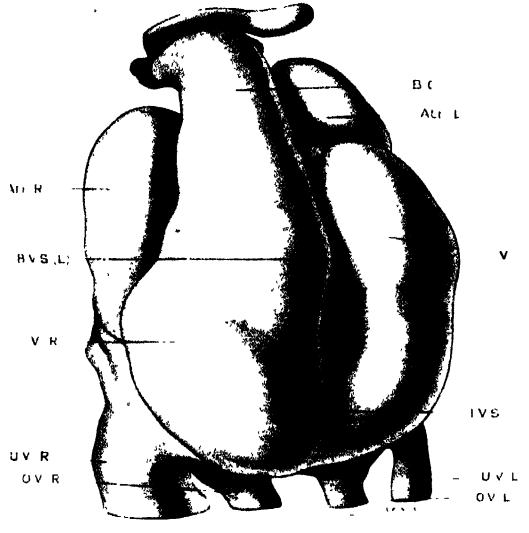


25.

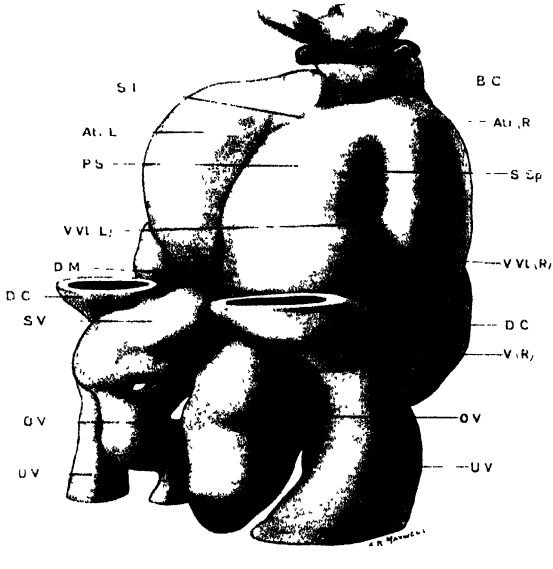


26

THE DEVELOPMENT OF THE HEART IN THE RABBIT.

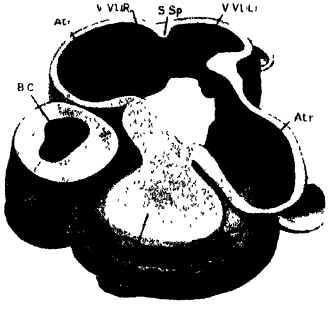


27

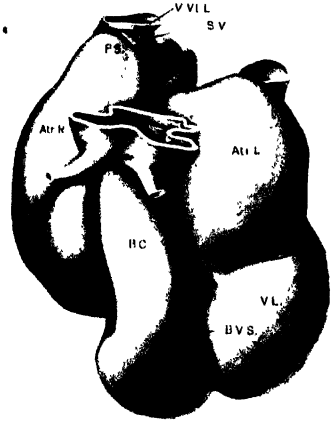


28.

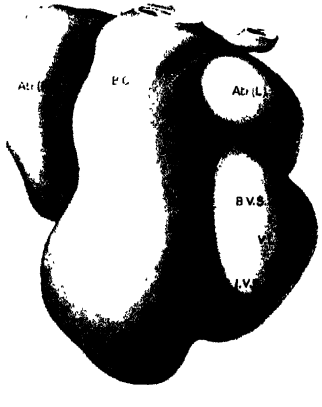
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



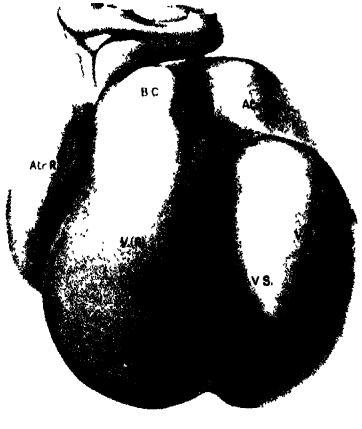
29.



30.

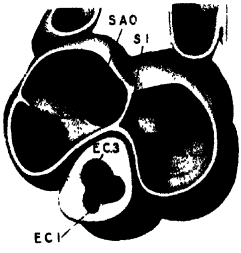


31.

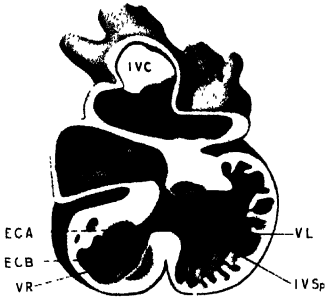


32.

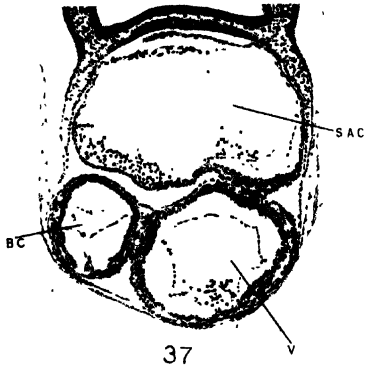
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



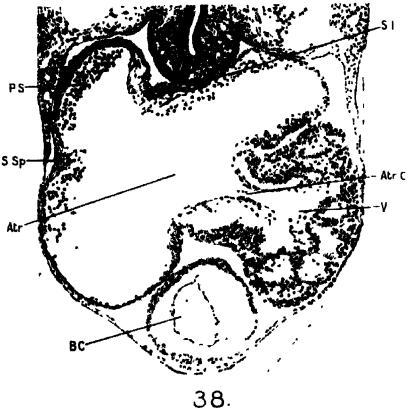
33.



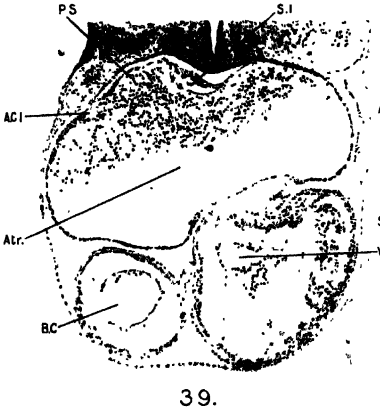
34.



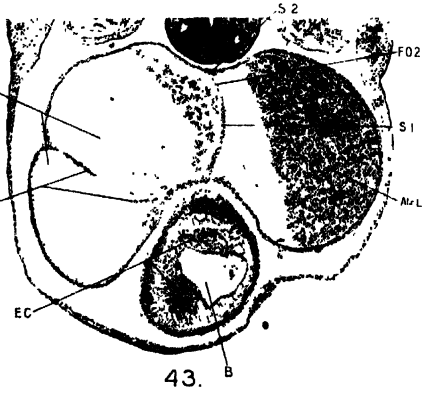
37



38.

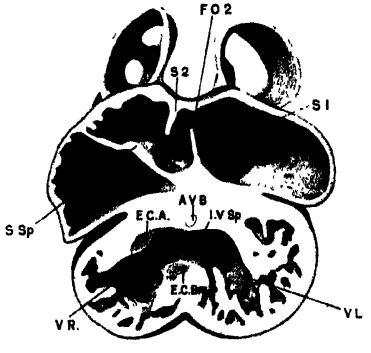


39.

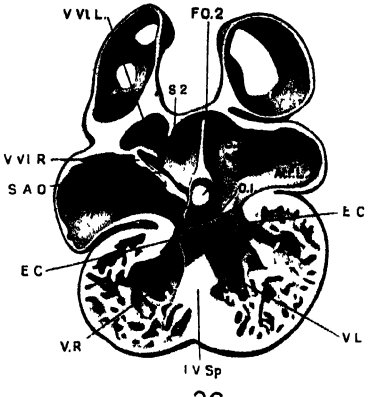


43.

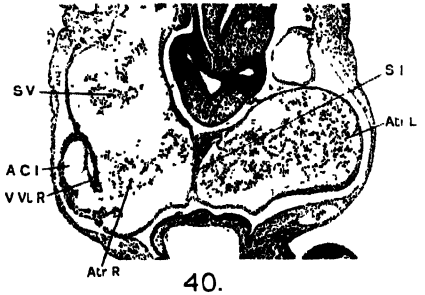
THE DEVELOPMENT OF THE HEART IN THE RABBIT.



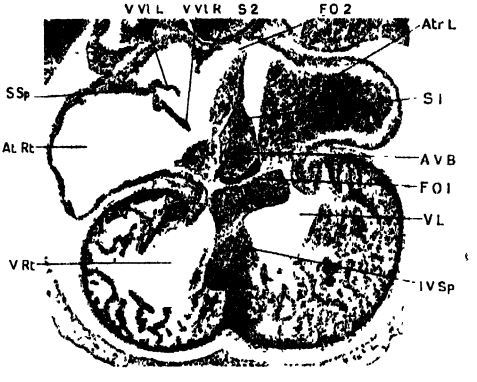
35.



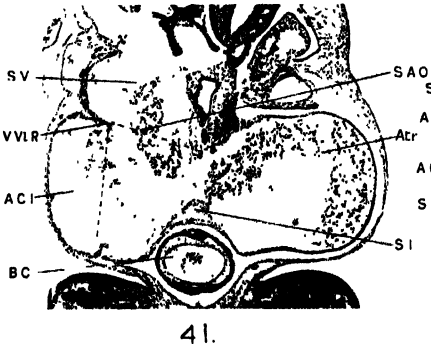
36.



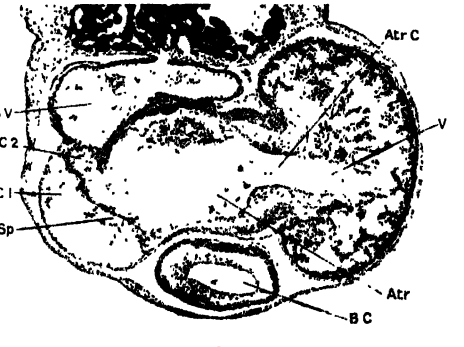
40.



44.



41.



42.

THE DEVELOPMENT OF THE HEART IN THE RABBIT.

34. The Development of the Heart in the Rabbit.

By A. Girgis, M.Sc. (London), M.R.C.S. (Eng.) *, Lecturer in Anatomy, Faculty of Medicine, Egyptian University, Cairo.

(From the Department of Anatomy and Embryology, University College, London.)

[Received May 20, 1930: Read June 3, 1930.]

(Plates I.–XI.†; Text-figures 1–4.)

Contents.

			Page
Introduction			755
Material and Methods			756
The Tubular Stage			757
Description of Models		I. and I. *a*	757
„	„	II. and II. *a*	758
„	„	III. and III. *a*	760
„	„	IV. and IV. *a*	762
„	„	V.	767
„	„	VI.	769
„	„	VII.	770
„	„	VIII.	772
„	„	IX.	774
„	„	X.	774
„	„	XI.	776
Summary			778
Conclusions			780
Bibliography			782

Introduction.

The early development of the mammalian heart has, in recent years, been studied by a number of investigators, including Katherine M. Parker (1915) on the early development of the marsupial heart, Schulte (1916) on the formation of the cardiac loop in the Cat, Wang (1917) on the earliest stages in the development of the heart in the Ferret, Murray (1919) on the development of the cardiac loop in the Rabbit, Yoshinaga (1921) on the early development of the heart in the Guinea-pig, K. M. Watson (1924) on the origin of the heart in *Felis*, and Davis (1927) on the early development of the heart in Man.

These more recent investigators have confined their attention very largely to the earlier stages in heart development, more particularly to the question of the origin and mode of fusion of the early heart-tubes and of the origin of the related vessels.

The classical paper of Born (1889) on the development of the rabbit's heart from the union of the cardiac tubes up to the adult condition, and Tandler's account (1912, 1913) of the development of the human heart still form the basis of our knowledge of the later stages of mammalian heart development.

* Communicated by Prof. J. P. Hill, F.R.S., F.Z.S.

† For Explanation of the Plates, see p. 780.

The origin and the early history of the endocardiac tubes have not been studied in this work. Starting with the stage when the heart-tubes have become approximated on either side of the mid-ventral line, my object has been to investigate the part they take in the formation of the different regions of the adult heart. The history of these tubes has been followed up to their fusion and disappearance as independent structures, *i. e.*, up to the stage when the four primary divisions of the heart, bulbus, ventricle, atrium, and sinus are well marked.

The description of the earlier stages in cardiac development is followed by an account of the later history of the primary divisions, which supplements in certain respects the account of the corresponding stages given by Born.

Material and Methods.

The material used for this paper consists of a series of rabbit embryos from the collection of Prof. J. P. Hill, F.R.S. I have studied over 100 embryos ranging in age from 8 to 15 days. It was due to this excellently prepared collection that I have been able to study stages at very short intervals. This is an important factor in studying the rapidly developing heart. The work was done in the Department of Anatomy and Embryology, University College, London, under the guidance of Prof. Hill, for whose valuable criticism and encouragement I am truly grateful.

The method used for studying the different stages is by wax-plate models and by serial drawings made by means of the Leitz projection apparatus. Twenty-nine models were made, of which fifteen will be described in this paper. These models are:—

Models I. and I. *a*, of R273C, 8 days 20 hrs., 10 somites, one model showing the myocardiac tubes, and the other model the endocardiac tubes alone.
Models II. and II. *a*, of R280D, 8 days 20 hrs., 11 somites, as above.
Models III. and III. *a*, of R278A, 8 days 20 hrs., 12 somites, as above.
Models IV. and IV. *a*, of R200, 9 days, 13 somites, as above.
Model V., of R253, 9 days, 10 hrs., 21 somites.
Model VI., of R275, 10 days, 18 hrs., 34 somites.
Model VII., of R6, 11 days, 39 somites.
Model VIII., of R6, G.L. 6 mm., 11 days.
Model IX., of R5–20, G.L. 7 mm.
Model X., of R5–20, G.L. 7·5 mm.
Model XI., of R*a*, G.L. 10 mm.

Four sets of serial drawings by the projection apparatus, showing the development of the right ventricle, were also made of the following embryos:—

R220, 10 days, 25 somites.
R217, 10 days, 31 somites.
R213, 10 days, 32 somites.
R212, 13 days, G.L. 8·5 mm.

The scheme which is followed in this paper is to describe the first four pairs of models, which represent what may be termed the tubular phase, then models V.–XI. inclusive, describing the different parts of the heart in each.

I interpolate here some remarks on the cardiac tubes before they approach each other in the middle line. Examination of the earliest stages (R192 & R184) demonstrates the presence of the middle cardiac plate and the angiocysts as observed by Mrs. Watson and Schulte in the cat's heart, and also affords confirmation of the contention of Mrs. Watson that Wang's "median heart rudiment" in the ferret has no existence in the cat. No such structure is present in the rabbit. I refer the reader to Mrs. Watson's criticism of Wang's statement.

It is not in the scope of this paper to discuss the fate and the function of the angiocysts, which according to Schulte help in uniting the two endocardiac tubes together, and according to Mrs. Watson represent a ventral aorta in the cat. According to Davis the middle cardiac plate, which persists in the human heart to the 7-somite stage, "appears to be taken up into the myocardial wall *pari passu* with the approximation of the adjacent cardiogenic folds." In the rabbit also the myocardiac layer of the plate is incorporated in the myocardiac mantle during the expansion of the heart and the fusion of the endocardiac tubes.

The Tubular Phase.

This phase, characterized by the presence of the two endocardiac tubes distinct from each other or partially fused, comprises the approximation of the two cardiac tubes in the middle line and the formation from them of a single heart-tube curved into two loops. About forty embryos of this phase have been studied, and four of them, showing progressive stages, have been modelled.

During this period, the development of the heart proceeds very rapidly. In the embryos examined, fusion is completed in about 4 hours, and during that period only 3 additional somite-pairs have appeared.

The originally paired myocardiac tubes give origin to the continuous myocardiac mantle some time before the endocardiac tubes have completely fused, so that in certain early stages, whilst the heart shows no external evidence of its paired origin, internally the endocardium may still be represented by two incompletely fused tubes. It should be noted that in using the expression "myocardiac tubes" it is not thereby implied that this structure is actually a complete tube. As a matter of fact, the myocardiac mantle can only be said to form a complete investment of the heart after the disappearance of the dorsal mesocardium. In the early stages the myocardium, whether paired or unpaired, is always incomplete on the dorsal side.

The figures of the first four pairs of models illustrate the changes that take place. Each pair consists of one model of the myocardium and one model of the endocardiac tubes of the same embryo. The first three pairs are of embryos of the same age, 8 days 20 hrs., but possessing 10, 11, and 12 somites respectively. The fourth pair is from an embryo 9 days old, with 13 somites. These embryos are very near each other in age and in the state of development of all other organs except the heart, which shows a marked difference as between the first and fourth.

Models I., I. *a*.

(R273C, 8 days 20 hrs., 10 somites.)

The Myocardiac Tubes (Pl. I. fig. 1).

These appear as two dilated tubes projecting into the pleuro-pericardiac cœlom, the long axis of each tube being slightly oblique to the median plane of the body. Each tube is marked out by two constrictions, one cranial and the other caudal. The former is narrower and more marked than the latter, and the right caudal constriction is more marked than the corresponding left.

Laterally each tube bulges freely into the pleuro-pericardiac cœlom. Medially the two tubes are in contact with each other cranially for about one-third of their length, but transverse sections show that the two adjacent walls are still separate. The remaining two-thirds of the tubes diverge gradually from each other in the caudal direction, so as to enclose a triangular space which is roofed in by the myocardiac layer of the middle cardiac plate. This plate serves to connect the two myocardiac tubes.

Cranially, at the cranial constriction the wall of each myocardiac tube ends by

passing over into the splanchnic mesoderm of the fore-gut. Caudally, the myocardiac wall is directly continuous with the similar layer around the endothelium of the corresponding vitelline vein.

The proximal portions of these veins have precisely the same constitution as the heart-tubes, and the question accordingly arises as to the location of the hinder ends of the latter. I have come to the conclusion that the caudal constrictions above mentioned mark the junction of the vitelline veins with the cardiac primordia—a conclusion which is supported by the condition in the succeeding stage.

Dorsally, the walls of the myocardiac tubes are connected across the middle line by the myocardiac layer of the middle cardiac plate, whilst laterally a short distance from the middle line they are reflected into the dorsal pleuro-pericardiac walls. At this stage the caudal half of each tube possesses what looks like a dorsal mesocardium of its own (Pl. V. fig. 14).

The middle cardiac plate, as already noted, reaches its maximum width between the caudal portions of the tubes and gradually decreases in width as it is traced forwards.

The wall of each tube is 2–3 cells thick, and is separated from that of the endocardiac tube by a space which is widest laterally and which is devoid of any kind of formed element.

The Endocardiac Tubes (Pl. I. fig. 2).

These are enclosed in the myocardiac tubes, and are separated from each other cranially by the thickness of the two adjacent walls of these tubes. Caudally they are much wider apart, and, like the myocardiac tubes, are bridged across by the endocardiac layer of the middle cardiac plate (Pl. V. fig. 14).

The tubes are somewhat pear-shaped, being wider cranially than caudally. At its cranial end each tube narrows abruptly in the region of the cranial constriction, and, bending round, passes into continuity with the corresponding first aortic arch, which runs transversely outwards.

Caudally, the narrower end of each tube is continuous with the corresponding vitelline vein, from which it is marked off only by the caudal constriction, as in the case of the myocardiac tube.

The wall of the endocardiac tube is composed of a single layer of very thin flattened cells.

Models II., II. *a*.

(R280D, 8 days, 20 hrs., 11 somites.)

The Myocardium (Pl. I. fig. 3).

There is a marked difference between this stage and the preceding one. The heart primordium has increased in size in all its dimensions, there being a slight increase in breadth and a very definite increase in cranio-caudal length and in dorso-ventral thickness as compared with Model I. Moreover, the heart is now beginning to lose the definitely paired character it exhibits in that model, though its constituent halves are still recognizable in ventral view through the presence of a sinuous groove along its ventral middle line. This groove begins cranially in the region of the future bulbus, where it is shallow; continuing back, it widens out into an irregular transverse depression, occupying the central region of the ventral surface, from which a wide approximately median groove runs back, to terminate in a deepish transversely disposed triangular depression at the caudal limit of the heart. The roof of this latter depression may still be said to be formed by the middle cardiac plate, but cranially to it that plate has been incorporated in the myocardiac mantle, the median groove and depression being all that is left

of the triangular space and groove which separated the myocardiac tubes in Model I. The myocardiac layer of the middle cardiac plate is accordingly to be regarded as being progressively incorporated in the myocardiac mantle from before backwards.

As we shall see when we come to deal with the endocardiac tubes, the expansion of the myocardiac walls, and in particular the evagination and incorporation of the myocardiac layer of the middle cardiac plate into the latter, are to be regarded as the result of the very marked increase in the size of these tubes.

The above-mentioned groove (Pl. V. figs. 15, 16, 17, I.S.R.) ends cranially at the level at which the endocardiac tubes join the first pairs of aortic arches. It may be called the "intertubular groove or sulcus." It is destined to disappear entirely.

The lateral parts of the two myocardiac tubes have expanded in opposite directions. The left has bulged out cranio-laterally, and in doing so an oblique groove running cranio-caudally towards the middle line has been formed between this expansion and the narrower medial part of the same tube. This groove is deepest laterally and is widely separated from the intertubular sulcus by the thickness of the narrow part of the tube. It is the first appearance of the left bulbo-ventricular sulcus (fig.3,B.V.S.(L.)). The right tube has expanded in a ventro-caudal direction, and in so doing has produced two effects: firstly, the caudal constriction has come to occupy a more oblique position as compared with its transverse disposition in the previous stage, and it has also become greatly accentuated; secondly, the expansion has come to lie ventral to the cranial end of the right vitelline vein (Pl. V. fig. 18, Vt.V.(R.)). This end of the vein has also undergone enlargement, and appears as a wide expansion lying dorsal to the caudal end of the heart. The left vitelline vein does not enlarge, and remains in the same plane as the left myocardiac tube, being separated from it by the caudal constriction of that side (Pl. V. fig. 18). This constriction, though definite, is much less marked than the right one.

Due to this diagonal expansion of the two tubes the greatest diameter of the heart shifts from the transverse position it occupied in the previous stage to an oblique position from left cranial to right caudal.

Dorsally, the myocardiac reflections come in contact with each other, and a true dorsal mesocardium is thus formed (Pl. V. figs. 16, 17).

The wall is still about 2-3 cells thick, and the space between the myocardiac and endocardiac walls is still present, but it is less than that of Model I.

The Endocardiac Tubes (Pl. II. fig. 4).

The cranial portions of the two tubes, marking the site of the future bulbus, are now in contact with each other, but their walls (Pl. V. figs. 15, 16, 17) in the sections are seen to be still intact.

Behind this region of contact the two tubes diverge, bending outwards to form huge dilatations. Caudally they become reduced in size and bend inwards slightly towards the middle line, then turn sharply outwards to become continuous with the vitelline veins. The caudal constriction, marking the junction of each tube with the corresponding vein, now appears very marked, partly owing to an actual narrowing of the tube in this region, partly to the expansion of the vitelline veins, the right vein being larger than the left.

In their detailed characters the endocardiac tubes exhibit changes corresponding to those already described for the myocardiac mantle. The expansion of the tubes in opposite directions is again seen here, but more obviously. The left dilatation possesses a very distinct cranio-lateral projection, whilst the right dilatation shows an even larger caudo-lateral projection, which in the ventral view of the model almost hides the right caudal constriction.

Whilst the cranial end of the left vitelline vein lies approximately in the same plane as the left endocardiac tube, the thicker right vein lies in a plane decidedly dorsal to that of the right tube.

The groove of the left bulbo-ventricular sulcus is well formed. The right is just indicated.

The median space between the caudal portions of the two tubes is bridged across by the endocardiac layer of the middle cardiac plate (not shown in the model).

Models III., III. *a*.

(R278A, 8 days, 20 hrs., 12 somites).

The Myocardiac Mantle (Pls. II. & III. figs. 5 & 6).

The heart has increased enormously in size—indeed, is about double the size of that of the preceding embryo.

When viewed from the ventral aspect the heart, though simple in character, exhibits the familiar heart-shape, and is seen to consist of a large swollen bulbous region, prolonged in front into a short cylindrical segment. The latter represents the bulbus cordis, the former the ventricular region. The latter is marked out into asymmetrical right and left portions by an oblique longitudinal sulcus which begins dorsally on the left side of the bulbus, so that the latter is actually continuous with the right ventricular bulging.

The sulcus is formed from two parts. The first and longer is the ventral extension of the left bulbo-ventricular sulcus shown in the previous stage (compare Pls. I. & II. figs. 3 & 5). It runs as mentioned, around the left side of the bulbus, towards the middle line, then continues caudally and obliquely over the ventricular surface until it reaches a much wider and deeper but shorter, almost median groove on the ventro-caudal surface of the heart. This forms the second part of the sulcus, and represents the caudal part of the intertubular sulcus between the two halves of the myocardium seen in the last stage (Pl. I. fig. 3). The cranial part of the same sulcus, which was visible on the ventral surface of the bulbus in the previous model, has disappeared in this stage, due to the expansion of the myocardiac mantle in that region.

This persisting caudal part of the intertubular sulcus corresponds to a ridge on the inner surface of the myocardium (Pl. VI. fig. 20, I.S.R.), but both are destined to disappear in the next stage. There the left bulbo-ventricular groove alone remains.

The intertubular sulcus has been mistaken by some authors for the inter-ventricular sulcus, but this only appears later, when the right ventricle begins to develop.

The bulgings on both sides of the median sulcus are formed by the dilatations, which have been described in the previous stage. Here they have expanded in practically all directions, and appear globular in shape when seen from the front. They overhang the caudal constrictions of the two tubes, hiding them from view, and to a much greater extent on the right than on the left side.

Due to the cranial expansion of the right bulging a short shallow groove has been formed between it and the bulbus. This is the first appearance of the right bulbo-ventricular sulcus.

Dorsal to the heart the vitelline veins can be seen (Pls. II. & III. figs. 5 & 6, Vt.V.). The left vein runs transversely and caudal to the heart. The right vein also runs transversely, but extends cranio-dorsally to the right ventricular bulging, and is larger than the left.

When seen from the left aspect (Pl. III. fig. 6) the left half of the heart appears pear-shaped in form. The thick part is formed by the large left ventricular bulging

(V) already seen in the ventral view. The narrow stalk-like region (Pl. III. fig. 6) is directed dorso-caudally and shows three well-marked oblique grooves on its surface. The most cranial (fig. 6, Atr.C.G.) is deep and narrow, and fades out as it is traced ventrally. It separates the left ventricular expansion from the narrow region of the left tube, and marks the site of the future atrial canal, whilst the bulging part of the tube immediately behind it represents the primitive atrium (Atr.).

The most caudal of the three grooves (Cd.C.(L.)) is shallow, and is formed by the lateral part of the caudal constriction of the left tube, separating it from the left vitelline vein, which lies caudal and lateral to the left tube.

Immediately in front of the caudal constriction, the caudal end of the left tube is slightly enlarged (E.L.T.) and is bounded in front by a wide shallow groove (the middle of the three grooves mentioned above), which also fades out below (G.L.T.). This enlargement in the next stage will be seen to have united with the caudal end of the right tube, with which the cranial end of the right vitelline vein is continuous. The enlarged caudal end of the left tube, the caudal part of the right tube, and the enlarged cranial part of the right vitelline vein together form the sinus venosus (Pl. VI. figs. 21 and 23). Thus, on the left side of this model we see half the primitive ventricle, all the primitive atrium, and a part of the primitive sinus venosus.

When examined from the right side, the model shows the large ventricular dilatation involving the whole of that side with the exception of the bulbus, with which it is continuous cranially, being separated from the same by the right bulbo-ventricular sulcus as described above.

It will be noted that the right and left lateral views of the model show decided differences, as indicated above.

Dorsal to the caudal portion of the right ventricular dilatation is the right vitelline vein, which differs greatly from the left in its size and relations. It runs forwards and inwards as a large trunk dorsal to the caudal portion of the right ventricular dilatation, from which it is separated by a deep obliquely horizontal sulcus in the position of the caudal constriction of the earlier stages. Medially it opens through the caudal end of the right tube into the enlarged caudal portion of the left tube, with both of which it will participate in forming the sinus venosus.

In sections (Pl. VI. figs. 20, and 21) the myocardiac mantle in the caudal half of the heart still shows evidence of its paired origin, but in the cranial half all traces of its original bilaterality have disappeared, and likewise the cranial part of the intertubular sulcus and the related internally projecting ridge (seen in Model II.) have disappeared.

The endocardiac tubes are still present in the bulbus, enclosed in the now single myocardiac tube (Pl. VI. fig. 19).

The myocardium is still about 2–3 cells thick, but the space between it and the endocardium is greatly diminished.

The Endocardiac Tubes (Pls. II. & III. figs. 7, 8, 9).

These have come in contact with each other throughout their length, but they are still distinct (Pl. VI. figs. 19, 20, 21). They have expanded in all directions, especially ventrally, so that their dorso-ventral diameter is more than half their cranio-caudal length.

The bulbar part of each tube has greatly diminished in diameter, but unequally, the left being much smaller than the right (Pl. VI. fig. 19, E.T.). The two parts are still distinct.

All the changes which have been described in the myocardium are shown more clearly in this model, especially the marked expansion of the right vitelline vein behind the right ventricular swelling. The groove denoting the future atrial canal between the left ventricular swelling and the narrow caudal

region of the left tube is wide and shallow. The middle groove is represented by a slight depression, separating the atrium from the sinus part of the left tube. The groove of the caudal constriction of the left tube is well marked, being accentuated by the projection of the sinus part of the tube.

In sections the adjacent walls of the two tubes are beginning to break down in places, but their contour is still recognisable in every section.

Models IV., IV. a.

(R 200, 9 days, 13 somites.)

The Myocardiac Mantle (Pl. IV. fig. 10).

The chief events in this stage are:—

(1) The disappearance of all traces of the intertubular sulcus.

(2) The dorsal and lateral expansion of the sinu-atrial region as the result of the growth of the hinder part of the left tube, the dorso-ventral diameter of the heart being now greater than the transverse and cranio-caudal diameters.

Viewed from the ventral aspect (Pl. IV. fig. 10) the bulbus is now seen to have shifted its position definitely to the right side of the heart, and now lies ventro-laterally. It is bounded on its left and right sides by the left and right bulbo-ventricular sulci respectively. The right sulcus (lateral in position as compared with the ventral position of the left and hence not visible in Pl. IV. fig. 10, though indicated in text-fig. 1) is now well marked, and corresponds to a definite infolding of the myocardiac mantle.

The bulbus is much longer than that of the previous stage. It has a transverse shallow groove on its left ventro-lateral surface, the significance of which is not clear. It is probably due to a twist as the bulbus increases in length, its cranial end being fixed in the roof of the pleuro-pericardial cavity, and its caudal end limited in its movement by the heart as a whole. This sulcus disappears entirely in all subsequent stages.

The left and the right bulbo-ventricular sulci are more marked in this model than in any of the models of the tubular stage, and so the bulbar region appears as an outstanding projection, on the right ventro-lateral surface of the heart. This is due to the fact that the bulbar parts of the endocardiac tubes in this model are of small diameter compared with the expanded myocardiac bulbus. The result is that the notch on either side at the junction of the bulbus with the dilated ventricular region is deep and sharply marked.

Viewed from the left side the groove denoting the atrial canal has become much shallower than that in the previous model, as the result of the great expansion which has taken place in this region, but it has increased in extent and can now be traced round on to the caudal surface of the left tube. It has also changed its direction, and now runs cranio-caudally (compare Pls. II. & IV. figs. 5 & 10).

The atrial and the sinus parts of the left tube now form a continuous expansion, the sinu-atrial region—the groove between them in the preceding stage having become obliterated, also, no doubt, as the result of the great growth which has taken place in this region of the tube.

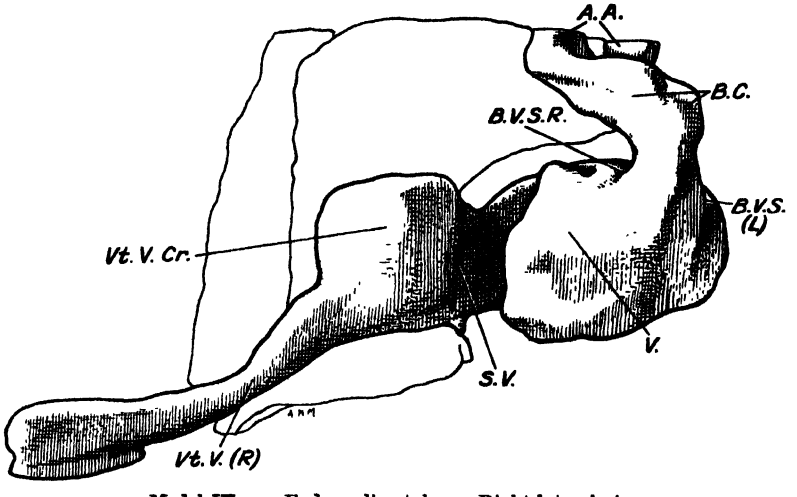
The left ventricular expansion has increased but little in comparison with the enormous growth of the sinu-atrial region.

Viewed from the right side (text-fig. 1), the expanded end of the right vitelline vein is seen to have increased markedly in size, and the greater part of it now lies dorsal to the heart. It is continuous by way of the caudal end of the right tube with the sinus part of the left tube, forming with it a large transverse cavity, the sinus venosus. This is continuous ventrally on the left side with the atrial part of the left tube without any demarcation (Pl. VI. figs. 22 & 23), so that at this stage there is present a single sinu-atrial cavity.

The bulbus is seen here occupying a ventral position, and between it and the sinus the right ventricular expansion appears (Pl. VI. fig. 22). This, like its fellow on the left side, has apparently remained stationary. The two ventricular expansions have now united to form the primary ventricle.

The sinus and the ventricle are separated from each other on the right side by a deep sulcus formed by the infolding of the myocardiac mantle, which extends inwards towards the middle line. The floor of the sulcus represents the caudal constriction of the right tube (Pl. VI. figs. 22, 23).

Text-figure 1.



Model IV. *a*. Endocardiac tubes. Right lateral view.

Dorsally the dorsal mesocardium has disappeared, except along the extent of the sinus venosus. This is an event which coincides with the appearance of the first cardiac loop; and as the length between the cranial and caudal limits of the heart has increased and its ends are more or less fixed, the disappearance of the dorsal mesocardium allows the formation of the loop.

The myocardiac wall is still 2–3 cells thick, and the space between it and the endocardiac wall is still present.

The Endocardiac Tubes (Pl. VI. figs. 11, 13, & text-fig. 1).

Fusion has advanced caudally, and the adjacent walls are breaking down in this region, but the two tubes are still distinguishable by a groove seen on the ventral surface of the bulbus and the ventricle (Pl. IV. figs. 11 & 13).

The transverse sulcus, which appears on the left ventro-lateral surface of the myocardiac bulbus, does not appear on the endocardiac bulbus. This may be due to the fact that the endocardiac bulbus is much smaller than the myocardiac one, and therefore is not affected by the twist, which may account for the presence of the sulcus on the latter.

The left tube has elongated in a dorso-ventral direction due to the great increase in size of its sinu-atrial part. The groove between its ventricular and bulbar regions is deep, and receives the fold of the left bulbo-ventricular sulcus.

The groove denoting the atrial canal is less marked than that of the myocardiac model.

The right tube has not increased nearly as much in size as the left—in fact, it is decidedly smaller,—and its expansion, though evident, is much less marked than in the previous stage. The groove between the ventricular expansion and the bulbar part of the same tube is shorter and less marked than its fellow on the left side, in correspondence with the condition of the right bulbo-ventricular sulcus, which is shorter and shallower than the left.

The sinus venosus is well established in this stage and is clearly seen in the model (Pl. IV. fig. 13, S.V.). Round its mid-region cranially and dorsally there runs a transversely wide depression, denoting the line of union of the cranial end of the right vitelline vein with the caudal end of the right endocardiac tube and the position of the right caudal constriction (Pl. VI. figs. 21, 23).

The sinus appears as a transversely elongated chamber lying dorsal to the ventricular region and extending from side to side of the pleuro-pericardial cavity, and in continuity with the atrium on the left side (Pl. VI. fig. 23). At either extremity, it is continuous on its caudal aspect with the corresponding vitelline vein. On the left side the caudal constriction is still very clearly seen between the sinus and the vein (fig. 13, Cd.C.(L.)).

In this stage the primitive parts of the heart are accordingly well established, and the contribution of each cardiac tube is as follows (see Pl. VI. figs. 21, 22, 23):—

The bulbus and ventricle are formed from both tubes.

The atrium is derived mainly from the left tube, and possibly in small part from the right one.

The sinus venosus arises from the enlarged caudal portion of the left tube, the caudal end of the right tube, and the expanded cranial end of the right vitelline vein.

Summary of Tubular Phase.

The outstanding features of the stages so far described may now be recapitulated.

The tubular stages in the development of the heart are passed through very rapidly. This rapid development can be realized from the fact that the interval between the approximation of the tubes and their fusion, if judged in time, is only 4 hours and, if judged by somites, is only 3 somites. During that interval the other structures of the embryo have advanced but little.

The myocardiac mantle is derived from the paired myocardiac tubes and the myocardiac layer of the middle cardiac plate, the latter layer becoming incorporated in the walls of the tubes as these expand coincidently with the enlargement of the endocardiac tubes. The original bilateral character of the myocardium soon disappears. In Model II. it is indicated by the sinuous median sulcus along the entire ventral aspect of the heart, whilst in Model III. the corresponding sulcus is represented only on the caudal half of the heart. This transitory sulcus we have termed the intertubular sulcus.

Model I. and I. *a* show that the cardiac primordium is represented by two dilated tubes lying one on either side of the middle line, and in contact with each other cranially over about one-third of their length. Each tube is marked out by two constrictions, one cranial and the other caudal, and consists of two layers—an outer incomplete myocardiac covering and an inner complete endocardiac tube. The two tubes are bridged across by the middle cardiac plate. This plate consists of two layers—a lower myocardiac, connecting the myocardiac tubes, and an upper endocardiac, connecting the endocardiac tubes. The endocardiac layer of the plate in some embryos shows cystic vesicles, the so-called angiocysts.

Models II. and II. *a* show that the intertubular sulcus between the halves of the myocardiac mantle is still present, though much reduced, and that the endocardiac tubes have come in contact over their cranial or bulbar portions

Expansion has taken place in the lateral walls of the tubes in opposite directions—the left cranio-laterally and the right ventro-laterally.

The left bulbo-ventricular groove has made its appearance.

The cranial and the caudal constrictions are well marked.

Models III. and III *a*. show the bulbar region as a single tubular structure containing two endocardiac tubes.

The left side of the heart is now distinguishable into two regions, a large ventricular expansion and a smaller caudal region. The latter is marked on its lateral surface by three grooves, the most cranial denotes the site of the atrial canal, separating the narrower caudal region from the ventricular expansion mentioned above. This narrower region is distinguishable into two parts by a groove (the middle one of the three); the cranial part becomes the atrium, the caudal part enlarges and unites with the caudal end of the right tube and the cranial end of the right vitelline vein to form the sinus venosus. This end of the vein enlarges and extends cranio-medially dorsal to the right side of the heart. The third groove is the lateral part of the left caudal constriction.

The endocardiac tubes are still distinct throughout their extent, though their adjacent walls are beginning to break down in places.

Models IV. and IV. *a* show the myocardic mantle in its fully expanded condition, the intertubular sulcus having disappeared. The right bulbo-ventricular sulcus is now established. The groove denoting the atrial canal, though shallow, has extended round the caudal surface of the left tube, and has changed in direction from an oblique dorso-ventral to a cranio-caudal position.

The two ventricular expansions unite to form the primitive ventricle. The atrial part of the left tube has increased in diameter and in length to form the primitive atrium.

The cranial end of the right vitelline vein has increased greatly in size and has come to lie dorsal to the heart. It is continuous through the caudal end of the right tube with the caudal end of the left tube, the three parts together forming the primitive sinus venosus.

The endocardiac tubes are fusing in a caudal direction, but their limits are still distinguishable.

Up to this stage the caudal constrictions of the two tubes are still clearly recognizable.

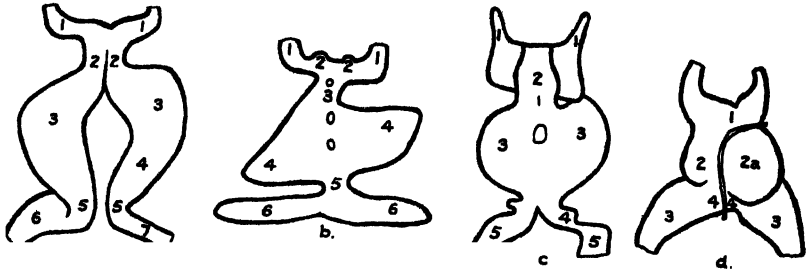
In reviewing the works of the various authors mentioned in the introduction, one is struck by the fact that practically all of them figure and describe the phase of mammalian heart development, which is represented in this work by Model II. *a* (Pl. II. fig. 4), in which the endocardiac tubes are definitely established as two distinct structures, lying in the same plane side by side in the pleuro-pericardiac cavity. The striking similarity in various mammalian hearts, including man, is brought out in text-figs. 2 & 3 which are diagrammatic reproductions from the figures of the authors referred to.

Their interpretation of the different parts of this stage is as striking in divergence as are the figures in resemblance. A study of the labelling of these figures will suffice to impress the reader with the extraordinary differences of opinion on such a fundamental stage in the development of the mammalian heart.

The outstanding difference among those authors is as to the location of the atrial canal. Murray in the rabbit, Mrs. Watson in the cat and marsupials, and Yoshinaga in the guinea-pig locate it at the caudal constriction of Model II *a*. Wang in the ferret locates it at the cranial constriction, whilst his lateral expansions are the atria. Schulte in the cat called the caudal constriction the atrio-venous angle, which is the nearest to our interpretation. Davis derives the ventricle from these caudal constrictions, and the bulbus from the expansions of the two tubes.

This divergence of interpretation is perhaps to be explained by the fact that

Text-figure 2.



a. Endocardiac tubes of model II. *a*.

1=aortic arches. 2=bulbus. 3=ventricle. 4=future sinu-atrial area and atrial canal. 5=caudal constriction. 6=right vitelline vein. 7=left vitelline vein.

b. Endocardiac tubes of rabbit (Murray's text-fig. 2).

1=aortic arches. 2=right and left bulbus. 3=bulbo-ventricular canal. 4=ventricle. 5=atrial canal. 6=vitelline veins.

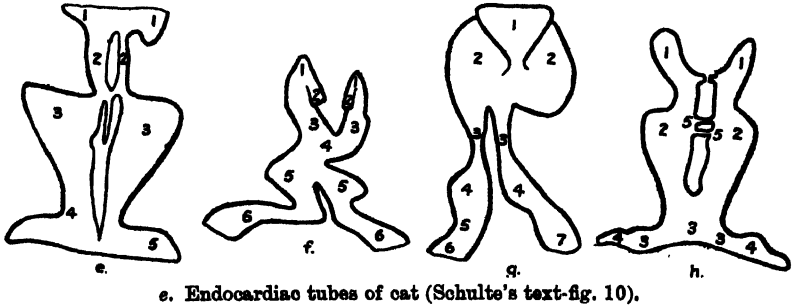
c. Endocardiac tubes of cat (K. M. Watson's text-fig. 12, dorsal view).

1=aortic arches. 2=bulbus. 3=ventricle. 4=atrium. 5=vitelline veins.

d. Model of marsupial heart (K. M. Parker's text-fig. 6).

1=bulbus. 2=ventricle (endocardium). 2 *a*=ventricle (myocardium), cut edge shown. 3=atrium. 4=atrio-ventricular constriction.

Text-figure 3.



e. Endocardiac tubes of cat (Schulte's text-fig. 10).

1=aortic arches. 2=bulbus. 3=ventricle. 4=atrio-venous angle. 5=vitelline vein.

f. Endocardiac tubes of ferret (Wang's text-fig. 31).

1=aortic arches. 2=dorsal aorta. 3=bulbus. 4=ventricle. 5=atria. 6=sinus venosus.

g. Endocardiac tubes of guinea-pig (Yoshinaga's text-fig. 23, dorsal view).

1=truncus arteriosus. 2=ventricle. 3=atrio-ventricular canal. 4=atria. 5=sinu-atrial constriction. 6=sinus venosus. 7=vein.

h. Endocardiac tubes of man (Davis's text-fig. 12).

1=aortic arches. 2=bulbus. 3=ventricles. 4=atria. 5=anastomosis between cardiac tubes.

none of these authors have followed the tubular stage of the heart to the stage of the adult condition.

Mrs. Watson, Wang, Yoshinaga, and Schulte ended their observations before the formation of the cardiac loop. Murray and Davis ended theirs at the formation of the loop, each interpreting the loop-stage on the basis of his interpretation of the stage mentioned above.

In Models III.–IV. *a* (see Pls. II., III., IV. figs. 5–13 & Pl. VI. figs. 21–23) the site of the atrial canal is first indicated by a faint groove some distance cranial to the caudal constriction. From this condition the atrial canal can be followed up to the definitive stage of the heart, as will be described in the following models.

The presumed location of the atrial canal in the caudal constriction must have as its result the formation of bilateral atria, as depicted in the figures of the above-mentioned authors. Davis (1927) states definitely in his conclusions, "The atria maintain their paired individuality." The atrium is certainly not paired in these early stages in the rabbit; it arises as a single cavity, and is only divided into two at a much later stage in development.

The left bulbar tube, according to Davis, disappears in man, and according to Schulte it becomes rudimentary in the cat. When Pls. II. & III. figs. 7 & 19 are compared with Pls. IV. & VI. figs. 11 & 22, it will be noticed that the left bulbar tube diminishes in the stage of Model III., but expands again in the stage of Model IV. This change in calibre of the left half of the bulbus may be due to changes in circulation at the two stages.

Model V.

(R253, 9 days 10 hrs., 21 somites.)

This model (Pl. VII. figs. 25, 26) is separated by a considerable gap from the preceding one. It represents a marked advance on the tubular stages we have hitherto been concerned with, inasmuch as the organ is now beginning to assume its definitive condition. The bulbo-ventricular loop has already been established, and has extended caudally, whilst the sinu-atrial region has grown to a very large size (Pl. VII. figs. 25 & 26).

Compared with Model IV. (Pl. IV. fig. 10), it will be noticed that the left ventricular dilatation has expanded enormously, especially in the dorsal and caudal directions, and at the same time it would appear to have undergone ventral rotation, so that its original cranial extremity (as seen in Model IV., Pl. IV. fig. 10) now occupies a point on the ventral surface.

The sinu-atrial region (situated in Model IV. dorso-caudally to the ventricular region) now lies cranially to the left ventricular lobe and dorsally to the right ventricular limb and the bulbus. This decided change in position has apparently resulted from the expansion of the sinu-atrial region in the cranial direction and its participation in the downward rotatory movement undergone by the left ventricular lobe. Its caudal part is embedded in the primordium of the septum transversum, and this no doubt limits its displacement and renders necessary marked growth in its dorsal wall.

As the result of these growth changes the region of junction (atrial canal) between the sinu-atrial and the left ventricular regions, from being cranio-caudal as in Model IV., now occupies an obliquely dorso-ventral position. This junctional region is marked on the ventral surface by a slight transverse depression separating the left ventricular and the sinu-atrial regions. The junction between these two regions is marked on the dorsal side by a deep sulcus, which corresponds internally to a well-marked fold, forming the dorsal margin of the opening of the atrial canal.

The formation of the definitive ventricular loop, characteristic of this stage, may be said to be the result of the caudal growth of the ventricular region and

the concomitant lengthening and deepening of the left bulbo-ventricular sulcus. The right ventricular limb forms the smaller right moiety of the loop, and has the form of a tapering cylinder, its narrower hinder end passing into continuity with the left limb by way of a short transverse segment.

The bulbus, continued forwards from the right limb, appears to be shorter than in the preceding stage. This is probably due to the taking up of part of the apparent bulbus of the preceding stage into the right ventricular limb. The bulbus is marked off from the latter limb by a deep dorso-lateral sulcus (the right bulbo-ventricular sulcus of the previous Model), but there is no definite line of demarcation between the two on the ventral surface.

The left bulbo-ventricular sulcus runs in a sagittal plane on the ventral aspect of the heart, separating the bulbus and the right ventricular limb from the sinu-atrial region and the left ventricular limb. It extends back to within a short distance of the caudal end of the heart, so that the two ventricular limbs are connected together caudally by a narrow transverse segment.

The dorsal region of the heart is formed by the sinu-atrial chamber, the caudal part of which lies embedded in the primordium of the septum transversum, and forms the transverse part of the sinus. Examination of transverse sections through this latter part shows that the cavity is provided with well-defined lateral expansions, of which the left is situated at a more cranial level than the right. These constitute the left and the right horns of the sinus, into which open the ducts of Cuvier and the umbilical and omphalomesenteric veins.

The right duct of Cuvier opens on the lateral aspect of the right horn, while the umbilical vein (lying dorso-laterally) and the omphalomesenteric (lying medio-ventrally) open side by side into its caudal aspect by what appears to be a common opening, though this is difficult to determine as they pass so gradually into the sinus cavity. Internally the opening of the right horn is defined by a semicircular ridge corresponding with an external groove.

Externally the left horn is definitely delimited from the rest of the sinu-atrium through the presence of a well-marked groove, which defines its cranial and dorsal limits, and which is in marked contrast with the shallow groove marking off the right horn. The left Cuvierian duct opens on its cranio-lateral aspect, while the other two veins open by a common opening on its caudo-dorsal aspect.

The cranial part of the groove above mentioned corresponds to a well-marked crescentic fold which defines the dorso-lateral margin of the opening of the horn into the sinu-atrial cavity. This fold is the first definite sign of the separation of the latter cavity into its two constituents. Born describes a similar fold in his first model of an embryo 9–9½ days, which resembles this model, but he states that the sinus is separated from the atrium all round at this stage by an external furrow, which is less distinct than that related to the fold in question. In our model, on the inner surface of the sinu-atrium there is a slight indication of a ridge continuous with, and on about the same level as, the crescentic fold, but it cannot be said for certain that this corresponds to Born's external furrow. It seems more probable that the division between the atrium and the sinus takes place by progressive extension of the crescentic fold mentioned above, rather than by the formation of a continuous encircling fold.

The dorsal mesocardium is still present in the caudal part of the sinu-atrial region. It reaches cranially to the level of the crescentic fold bounding the opening of the left horn.

Viewed from the interior the bottom (caudal wall) of the sinu-atrial cavity is seen to be divided by a sagittal ridge into two depressed areas, of which the right is larger than the left.

The atrial canal is situated in the cranio-ventral corner of the sinu-atrial cavity, and leads into the left ventricular limb. Its lumen is transversely oval and runs cranio-caudally.

The myocardiac wall of the sinu-atrial cavity is thin (Pl. X. fig. 37) and is in contact with the endocardium. In the ventricles and the bulbus the myocardiac wall is thicker, 3–4 cells, and is separated from the endocardiac wall by a space.

The cavities of the ventricles are joined together by a transverse passage, the ostium interventriculare. The ventricles differ from the bulbus in possessing thicker walls and in having the myocardium and endocardium more approximated and more irregular (trabeculated) in character, a condition associated with active growth.

Model VI.

(R275, 10 days 18 hrs., 34 somites.)

This stage (Pl. VIII. figs. 27, 28) is characterized by the division of the sinu-atrial cavity into atrium and sinus venosus. The cavity has grown to a very large size, and, indeed, it would seem to attain its maximum in this stage.

Viewed from the ventral aspect the bulbus is now seen to occupy a nearly median position. It is elongated, and its horizontal part has largely straightened out. The right ventricle now established forms the most ventral part of the heart. This ventral displacement of the right ventricle and the bulbus is due to the rotation of the heart on a longitudinal axis from right to left, and probably also to the great ventral expansion of the atrial cavity.

The right ventricle extends more caudally than the left, and the transverse part which joins the two ventricles is indented by a shallow longitudinal sulcus. This is the beginning of the interventricular sulcus. It is directly continuous with the left bulbo-ventricular sulcus.

On the left side of the bulbus, in the angle between the cranial end of the left ventricle and the cranial part of the left atrium, part of the wall of the atrial canal, now definitely established, is just visible (Pl. VIII. fig. 27). It now runs obliquely in a dorso-medial direction, its change of direction in this stage as compared with the preceding being due to the longitudinal rotation of the heart from right to left. On the right side of the bulbus the right atrium has expanded ventrally. The part of the atrium which lies in contact with the bulbus is indented by the latter.

When viewed from the left side the left ventricle appears as a pear-shaped eminence, its wider end being directed cranially and its longer diameter being dorso-ventral. The left atrium fits as a halfmoon-shaped structure on its dorso-cranial surface, and the left horn of the sinus fits on its dorso-caudal surface. The transverse part of the sinus is imbedded in the septum transversum caudally to the ventricle.

Between the left half of the atrium and the sinus the sinu-atrial constriction, which was just beginning in the last model, has become a deep wide cleft. The fold so produced cuts off the left half of the atrium from the sinus, so that the caudal wall of that part of the atrium turns in and forms its own floor. This fold is continuous medially, with a crescentic infolding of the ventral wall of the sinu-atrial cavity which separates the right half of the atrium from the sinus. When this fold reaches the right lateral wall (Pl. VIII. fig. 28) it takes a dorsally curved course on that, and finally, bending almost at a right angle, it runs on the dorsal wall, and fades out a short distance from the dorsal mesocardium. A well-marked sulcus on the surface of the lateral wall marks its position. In this way we have formed, from left to right, a semicircular fold separating the atrium from the sinus, and widest where it projects from the ventral wall. The opening thus formed between the two cavities is situated on the right side of the middle line, and when viewed from the atrial side is seen to face cranio-ventrally.

The just-described semicircular fold, although continuous at this stage, may be divided into two segments, viz., the segment bounding the opening ventrally and as far laterally as the right-angled bend, and that bounding it latero-dorsally

above the bend. The former is the primordium of the right venous valve and the latter that of the left. The right valve primordium is more developed than the left, and lies caudally to it.

On the lateral wall of the atrium, and starting at the angle marking the junction of the right and left valves, a longitudinal sulcus (Pls. VIII. & IX. figs. 28, 29, *s. sp.*) runs cranially towards the sagittal inbaying produced by the lodgement of the bulbus on the cranial wall of the atrium. This sulcus corresponds to a ridge on the inner surface of the atrium. Born in the rabbit and Tandler, in the man, regard this ridge as the beginning of the septum spurium. According to my observations, a cavity appears at a later stage in this ridge (Pls. X. & XI. figs. 39, 40) and opens into the atrium. The medial wall of this cavity will form the true septum spurium.

The septum primum makes its first appearance in this stage. It has the form of a horseshoe-shaped ridge which begins on the dorsal wall of the atrial cavity in the middle line, a short distance in front of the sinu-atrial opening, and runs obliquely forwards and to the right on the cranial wall, and then continues on to the ventral wall, to terminate behind the caudal end of the atrial opening of the atrial canal. Its cranio-ventral half coincides with the infolding produced by the lodgement of the bulbus. The myocardiac and endocardiac layers of the septum are markedly thickened, especially the endocardium, the thickening of which forms a broad rounded border, most distinct in the dorsal and ventral parts of the septum.

The cranio-dorsal region of the right atrium (Pl. VIII. fig. 28, P.S.) is marked off by three sulci, corresponding internally to the primordium of the septum spurium ventrally, the left venous valve caudally, and the septum primum medially, and constitutes the "pars interseptale" described by Born in the rabbit and by Tandler in the human heart.

On the dorsal surface of the heart the left horn of the sinus has separated from the left atrium (Pl. VIII. fig. 28, S.V.). It lies in a vertical position and is very much smaller than the right horn. The left umbilical and omphalomesenteric veins are also greatly reduced in size. The right horn is very large and extends much more cranially than the left. The corresponding veins are very large, the umbilical being larger than the omphalomesenteric. The transverse part of the sinus is extensive, and still occupies a caudal position immediately dorsal to the apical portion of the ventricle. The left duct of Cuvier has now shifted dorsally, and opens on the cranio-lateral aspect of the left horn. The right duct is still largely lateral, and opens some distance behind the cranial end of the right horn. The opening of the left Cuvierian duct is still somewhat in front of that of the right.

It remains to be mentioned that the lumen of the atrial canal is now slit-like, with slightly enlarged ends. It is disposed obliquely, its caudal end being more medial, its cranial end more lateral.

The myocardiac wall of the ventricles is thickened and trabeculated, and is in contact with the endocardium. The myocardium of the bulbus is still about 2-3 cells thick, and is separated from the endocardium by a space, void of tissue.

Model VII.

(R6, 11 days, 39 somites.)

The most important alteration which has taken place in this Model (Pl. IX. fig. 30) is the change in the position of the atrium and the sinus venosus in relation to the ventricles. Hitherto the atrium and the sinus were situated dorsally to the ventricles, the ventral walls of the atrium and the transverse part of the sinus being actually in contact with the dorsal wall of the ventricles. In

this stage the atrium lies cranial to the ventricles and the sinus is placed entirely dorsal to the atrium.

Born (pp. 300–301) explains the change in position of these parts as due to the more marked growth of the lower (caudo-dorsal) part of the ventricles and the upper (dorso-cranial) part of the atrium, combined with a rotation of the atrium in a cranio-ventral direction round a transverse axis, passing through the atrial opening of the atrial canal. With this explanation we are in agreement.

The ventricles have increased in size, the right in particular having become more bulbous, and their dorsal surfaces are now quite exposed. The right ventricle is still much smaller than the left, and forms the apex of the heart.

The interventricular sulcus is greatly deepened, especially at its caudal end, and the transverse segment now occupies a dorsal position.

The bulbus is now almost straight, and passes over below without any definite demarcation into the right ventricle.

The atrial canal, with an oblique cranio-caudal disposition, is seen midway on the left side of the bulbus, between the atrium and the left ventricle.

Very marked changes have taken place in the sinu-atrial junction. The sulcus which corresponds to the left venous valve, and which occupied a transverse position in the previous model, has now shifted to a cranio-caudal plane, and now lies in line with the sulcus of the right valve. This shifting is partly due to the rotation of the atrium and partly to the great reduction of the pars interseptale, which now appear as a small outpouching on the cranial and medial surface of the right atrium. The ridge representing the left valve and the corresponding sulcus have also extended medially, but have not yet met the medial end of the right valve. The result of the shifting of the left valve to a cranio-caudal plane is that the sinu-atrial opening now faces cranio-caudally, and the right valve is behind (caudal to) the left.

Another result of the rotation of the atrium is the shifting of the ridge which forms the primordium of the septum spurium to a dorso-ventral position on the cranial part of the lateral wall of the right atrium. The external sulcus has been obliterated, but the corresponding internal ridge is now greatly thickened. Its caudal part has been hollowed out by a cavity which opens into the atrium (Pls. X. & XI. figs. 39, 40, A.C.1.) in such a way that the medial wall of the cavity is left as a flap-like fold which is continuous near its lower attached end with the right venous valve. We were at first inclined to regard this flap as the beginning of the septum spurium, but the latter is not definitely formed until the next stage.

The sinus venosus is greatly reduced in size, especially the left horn, and the whole lies dorsal to the atrium. The ducts of Cuvier are definitely dorsal in position; the left is the smaller and opens into the cranial end of the left horn, and the right is large and opens just above the cranial end of the right horn. The right horn still lies much more cranial than the left.

The Interior of the Heart.

The sinu-atrial opening is smaller than in the previous model, and is now more definitely bounded, the venous valves being more developed, but on the medial side the medial ends of the two valves are still wide apart.

The wall of the sinus is about 2 cells thick, and does not show the thinning which accompanies rapid expansion as in Model VI.

The septum primum (Pl. XI. fig. 40, S.I.) has extended considerably in the caudal direction, and now forms a sagittal partition, dividing the cranial part of the atrium into right and left atria.

The atrial opening of the atrial canal is oval and is disposed obliquely in the horizontal plane.

The infolding of the ventral wall of the atrium produced by the bulbus is more marked, and runs sagittally through the whole extent of that wall from the septum primum cranially to the caudo-medial limit of the atrial opening.

As already described, the ridge-like thickening which gives origin to the septum spurium and which begins at the junction of the left and the right valves is now very distinct, and its caudal part has been hollowed out by a cavity opening into the atrium.

The region of the atrial wall which lies behind this cavity is also thickened and its inner surface is quite rough and irregular, a condition to be associated with active growth. It should be noted that the ridge-like thickening from which the septum spurium takes origin and the thickened area caudal to it are both parts of one continuous thickening.

The left atrium which is expanding more slowly is devoid of any such thickened area of its wall, and its surface is smooth.

In the ventricles the deep caudal end of the interventricular sulcus corresponds internally to a thick round fold separating the ventral parts of the two ventricles, dorsal to which they are in free communication.

The endocardiac lining of the ventricles lies in close contact with the myocardium, where it is in active growth, as indicated by the presence of trabeculæ, but is separated by a space in the areas where the myocardium is about 4 cells thick and devoid of trabeculæ.

In the bulbus the endocardium is separated from the thick myocardium by a space in which the endocardium is just beginning to thicken to form the endocardiac cushions.

Model VIII.

(R6, 11 days, G.L. 6 mm.)

The chief changes which have taken place in the heart represented by this model, of the same age as the preceding one, are associated with the venous valves, the septum spurium, and the thickened area of the atrial wall.

The latter area has increased in extent, more especially cranialwards, and as the result the septum spurium is now more caudally situated and lies practically in the same plane as the ventral portion of the right venous valve, with which, as well as with the left, it is continuous. The septum is now definitely formed and appears as a horizontal shelf-like fold which arises from the thickened area of the ventral wall, a short distance from the middle line. Just before it becomes continuous with the venous valves it is separated from the atrial wall by an oval depression, opening forwards.

Almost immediately behind the attachment of the septum to the valves a second cavity with a large irregular opening is present in the thickened area of the wall. The formation of such cavities in the myocardium of the latter area and in that of the developing septum spurium has been observed in all the 11-day embryos examined (10 in all) and in some early 12-day embryos, and must be regarded as a perfectly normal phenomenon. Its precise significance is not entirely clear, but since the cavities always open out into the atrial lumen it may be suggested that they serve to increase the size of the latter, whilst in the case of the septum spurium the appearances seen in the models and in sections strongly suggest the view that the septum really represents the persisting floor of such a cavity.

From the point of view of phylogeny the speculation may be permitted that the mammalian atrium consists of two parts, viz., the primitive atrium, comprising the part medial to the septum spurium, and a secondary addition situated laterally to and including the septum, this latter part forming at the expense of the thickened area of the atrial wall which is situated in the region of the sinu-atrial junction. This may perhaps be explained by the fact that in the tubular stage

(Pl. VI. fig. 22) the atrium arose mainly from the left endocardiac tube, whilst the contribution from the right tube is very small. The formation of the accessory cavities described above may possibly be regarded as an additional contribution from the right tube, since the area from which they arise corresponds morphologically to the sinu-atrial junction of Pl. VI. fig. 22.

The ventricles have increased in size, having extended in the dorso-cranial direction. Their dorsal walls are still continuous, *i. e.*, there is no external demarcation between them. The interventricular sulcus has deepened, and the right ventricle has grown further caudally as compared with the preceding stage.

The bulbus has shortened and increased in transverse diameter.

The horns and the transverse part of the sinus venosus now lie in the same transverse plane.

In the interior of the heart the left venous valve is much more developed, having the form of an elongated flap-like fold of the lateral wall attached precisely along the junction of the right horn of the sinus with the thickened area of the wall of the right atrium, which is marked externally by a well-defined sulcus. The valve extends on to the inner surface of the cranial wall, and gradually becomes reduced in height without reaching the medial extremity of the right valve. At its hinder end it is continuous ventrally with the septum spurium, and dorsally with the right valve.

In the preceding stage practically only the cranial portion of the left valve was laid down. In the present stage this cranial part has increased somewhat in width, whilst the lateral part may be regarded as a new formation. It is noteworthy that this lateral part arises at the same time as the septum spurium, and it seems probable that both structures are derived from the persisting wall of an accessory cavity that appeared in the thickened and actively growing zone of the right atrial wall, the septum spurium representing the persisting caudal wall and the lateral part of the left valve the persisting dorsal wall.

The right valve forming the caudo-medial boundary of the sinu-atrial opening has increased in width. It is situated medially to the left valve and is continuous with the caudal end of the latter, and at the same time with the septum spurium.

The point should be emphasized that the left venous valve at this stage is situated on the cranial and right side of the sinu-atrial opening, whilst the right valve forms the caudo-medial (left) boundary of the opening, so that the valves are reversed as compared with their final position.

The atrial canal is in the same oblique position as in the preceding stage, but it is compressed ventro-laterally, due to the appearance of two endocardiac cushions, respectively dorsal and ventral.

The interventricular fold has extended dorsally and to the left. The ostium interventriculare has narrowed, and still occupies a dorsal position.

Endocardiac cushions.—These are now definite structures in this stage, whereas in the preceding one they were represented by scattered endocardiac cells in the sub-endocardiac space (Pl. X. fig. 38). There are two sets.

The atrio-ventricular cushions (Pl. XI. fig. 42) are two disc-like pads, one on the dorsal, the other on the ventral side of the cleft-like atrial canal (Atr C.), and extending for a short distance on the inner surfaces of the atrium and ventricle.

The bulbar cushion surrounds the bulbar cavity along its length, but is incomplete on the left side, thus appearing horse-shoe shaped in cross-section. The cushion begins cranially where the bulbus enters the pharyngeal wall, and ends caudally at its junction with the right ventricle. It is thicker at its cranial end. Caudally it is less marked, and the connecting-piece of the horse-shoe is thinner than the two limbs.

Model IX.

(R 5–20, 7mm.)

A few changes are worthy of mention in this stage.

The right atrium shows a definite increase in size and has expanded laterally and cranially. The septum spurium has almost trebled in breadth as compared with that of the preceding stage. The free marginal portion of the septum is relatively thin and smooth, its remainder, on the other hand, is very thick and shows on its cranial surface a deep depression with an irregularly corrugated floor. This part has evidently been formed by cavity-formation from the actively growing wall, and towards its dorsal extremity actually shows a small perforation. Caudally the thickened part of the septum is directly continuous with the ventral lip of a second cavity, which corresponds to that seen in the preceding model, but is now much larger. The cavity opens widely into the right atrium, possessing a semicircular lip, and the whole structure looks like a semilunar valve.

The sinu-atrial opening has narrowed considerably, and the left valve has extended medially and has become continuous with the medial end of the right valve. The opening is now pear-shaped, and lies obliquely, so that when viewed from the sinus side it faces medially and to the left.

The ventricles have increased in size, and their junction is now marked on the dorsal surface by a shallow sulcus.

The atrial canal is no longer visible on the ventral surface of the heart, owing to the ventral expansion of the left ventricle.

Compared with Born's models, my Model VII. corresponds closely to his model 4, whilst my Model X. corresponds to his model 5. Models VIII. and IX., in which that curious development of accessory cavities in the thickened area of the right atrial wall occurs, are not represented in Born's series. Indeed, the gap between his models 4 and 5 is very considerable so far as the development of the septum spurium and the venous valves is concerned. The fact that neither Born nor Tandler make mention of these accessory cavities may be explained by the circumstance that the thickened area of the wall in which they appear is distinguishable only during a very short period, and so may quite easily be missed.

Model X.

(R 5/20, 7·5 mm.) (Pl. IX. fig. 31.)

The stages of heart-development represented by Models X. and XI. have already been described by Born and modelled by him (his models 5–7), and nearly corresponding stages of the human heart by Tandler and Waterston (figs. 5 & 12).

The sinus venosus has diminished in size and occupies a dorso-caudal position, above the atria.

The two atria (Pl. X. fig. 33) are delimited dorsally and cranially by a shallow, broad, sagittal sulcus, and ventrally by a deep sagittal notch occupied by the bulbus.

The right ventricle has expanded ventrally, and still forms the most caudal part of the heart. The left ventricle has expanded in a cranio-ventral direction, pushing the left atrium into a cranio-dorsal position. The interventricular sulcus has extended cranially on the ventral surface of the heart (Pl. X. fig. 34), replacing and coming into line with the left bulbo-ventricular sulcus.

The bulbus has shortened and increased in size. It is now more or less circular in cross-section, and fits in the median notch between the ventral parts of the two atria.

In the interior of the heart the inferior vena cava is seen opening into the

caudal part of the right horn (Pl. X. fig. 34, I.V.C.), in line with the sinu-atrial opening. The left horn is much smaller than the right, and the transverse part of the sinus is reduced.

The sinu-atrial opening, still pear-shaped, has changed in direction. Viewed from the sinus, it looks medially and to the left as in the preceding stage, but its lateral extremity, to which the septum spurium is attached, has moved cranially, as the result of the cranial expansion of the lateral part of the right atrium. At the same time the receding of the sinus to a more caudal position has carried the medial ends of the valves in the same direction. In a later stage, this rotation of the sino-atrial opening is continued until it becomes nearly sagittal in position.

Hitherto the right atrium has increased in size mainly by the growth of its ventro-lateral region, while the part that lies be ween the septum spurium laterally and the septum primum medially, viz. the pars interseptale, has grown but little. In this stage the pars interseptale has expanded chiefly in the transverse direction. The result of this expansion is that the septum spurium is displaced laterally. It now runs obliquely in a latero-medial direction (Pl. X. fig. 33, S.Sp.) instead of being horizontal as in the preceding two models. Moreover, its base of attachment has been perforated by a large irregular oval fenestra, precisely as in Born's model 6. It will be remembered that in the preceding stage only a quite small perforation was present.

Its cranial surface is continuous with the atrial surface of the left valve; its caudal surface is continuous with the atrial surface of the right valve. Its caudal border is directed caudo-medially, and is on the same level as the cranial end of the sinu-atrial opening.

The septum primum has increased in width, and in its dorso-cranial corner there is now present a small perforation, the beginning of the secondary foramen ovale (Pl. X. fig. 43, S.I., F.O.2).

The primary foramen ovale is now well defined and lies in the sagittal plane. Its cranial border is formed by the septum primum, and its ventro-caudal border by a broad band of endocardiac tissue, which is continuous with the ventral endocardiac cushion round the atrio-ventricular canal, as will be described in the next stage.

The atrio-ventricular canal (the primitive atrial canal) has become transverse in position, its ends being expanded. It opens into the cranio-dorsal corner of the interventricular opening, its larger part lying to the left of the middle line.

Endocardiac cushions.—In the last model the dorsal and ventral endocardiac cushions were already established on the ventral and the dorsal walls of the atrio-ventricular canal, which was then in an oblique position. In this stage the opening has become transverse and the two cushions have united laterally, forming a horse-shoe with its free ends directed medially and its closed end towards the left. The ventral cushion has also extended cranially at the junction of the two atria so as to form the ventro-caudal border of the primary foramen ovale.

In the bulbus the bulbar cushion (Pl. X. fig. 43, B.C.) is seen as a horse-shoe-shaped band running along the length of the bulbus, the free ends being towards the left. In this stage, two changes have taken place: (1) the horse-shoe has divided, except in its cranial region, into two bands; (2) the two bands have undergone a spiral twist. Cranially cushion 1 is ventro-lateral and cushion 3 is dorso-medial, whilst caudally cushion 1 is dorsal and cushion 3 is ventro-medial. They have also extended for a short distance into the right ventricle, where cushion 1, now forming proximal cushion A, is dorsal and cushion 3, now proximal cushion B, is ventro-medial.

Model XI.

(R *a*. G.L., 10 mm.) (Pls. IX. & XI. figs. 32, 35, 36, 44.)

The chief changes that have occurred in the external appearance of the heart in this stage (Pl. IX. fig. 32) are as follows:—

The right ventricle has increased still further in size, partly at the expense of the caudal end of the bulbus. The left ventricle also has expanded in the ventral and cranio-caudal directions, and now forms the apex of the heart, whilst the left atrium has been displaced to a dorsal position. The right atrium has expanded in a dorso-ventral direction, so that the latter now projects some distance in front of the former.

The sinus venosus has considerably diminished in size and occupies a position caudal to the atria.

In the interior of the heart still more marked changes have taken place. The sinu-atrial opening has been carried to a caudal position by the receding of the sinus in that direction. The opening (Pl. XI. fig. 36, S.A.O.) is now a slit-like aperture disposed obliquely from right dorsal to left medial.

The two venous valves have now reached their definitive condition. They are thin and project freely into the right atrium, their cranial portions curving forwards to become continuous with the septum spurium, which now lies in the same oblique plane as the valves. The left valve is shorter than the right, and has a notch on its free border. This notch faces the secondary foramen ovale, and no doubt helps the right valve to direct the blood through that opening.

The venous valves, it should be noted, have in this stage completed their process of rotation, so that the left valve, originally cranial on the right, is now situated medially and on the left of the sinu-atrial opening, whilst the right valve, originally caudo-medial and left, now forms the right boundary of the opening.

The wall of the right atrium (Pl. XI. fig. 35) has thickened and has developed trabeculæ, especially in its cranial part. The septum spurium is now very extensive and shows only two quite small perforations, in marked contrast with the huge perforation present in it in the preceding stage. Its position is marked on the surface by a shallow sulcus.

The secondary foramen ovale (Pl. XI. fig 35, F.O.II.) has now increased in size, and at the same time the primary foramen has been reduced to a transverse slit-like channel situated in the A-V endocardiac tissue at the ventral attachment of the septum primum.

The septum secundum (text-fig. 4) appears in a younger stage (embryo G.L. 8·5 mm.) than the one under consideration as a thickening on the right side of the cranio-dorsal attachment of the septum primum, as described by Born and Tandler. As this attachment begins to break down to form the secondary foramen, the new septum grows caudally and ventrally into the right atrium in a sagittal plane, diverging to the right from the primary septum (Pl. XI. fig. 35, S.2). In this model the septum secundum is seen as a well-developed flap extending from the dorsal wall of the right atrium a short distance to the right of the septum primum.

The only noteworthy advance in the left atrium is the appearance of the opening of the pulmonary vein at the root of the septum primum, midway between the ventral and dorsal walls of the atrium (Pl. XI. fig. 36).

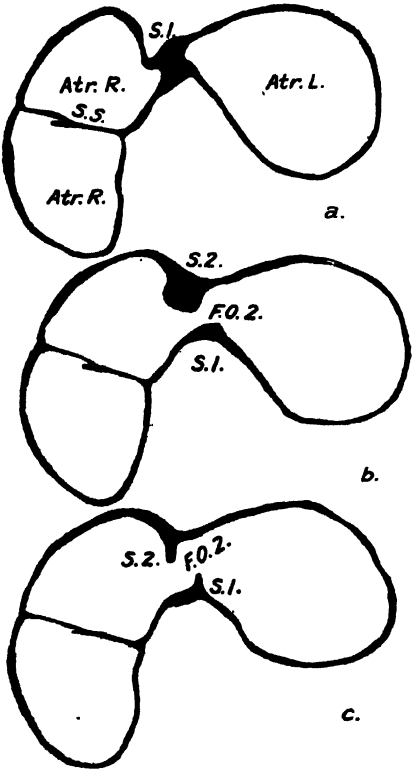
In the ventricles the interventricular foramen has narrowed considerably, as the result of the growth of the interventricular septum and the thickening of the endocardiac cushions.

The right ventricle has expanded still more in a cranial direction at the expense of the bulbus. The cranial part of the latter has become divided into ventral pulmonary and dorsal aortic channels by the union of endocardiac cushions 1 and 3.

Endocardiac cushions (Pl. XI. fig. 44).—In the preceding stage the dorsal and ventral atrio-ventricular cushions had united with each other laterally, and the

ventral cushion had also extended cranially on to that part of the atrial wall bounding the primary foramen ventrally. In this stage the cushions have extended towards the right so as to enclose the right end of the A-V opening, and their median portions have fused together so as to obliterate the middle part of the original transverse A-V opening, thus leaving its expanded extremities open as the definitive right and left A-V openings. In addition, in the interval between this and the preceding stage, the dorsal cushion has extended for some distance cranially on the dorsal atrial wall bounding the primary foramen ovale, the ventral

Text-figure 4.



Camera-lucida drawings, showing the development of the septum secundum in a 13-day embryo (G.L. 8·5 mm.).

a=sl. 7, 4, 6; b=sl. 7, 4, 8; c=sl. 7, 4, 10.

cushion having already correspondingly spread on the ventral atrial wall in the preceding stage. With these extensions, the endocardiac tissue on the crescentic free edge of the downwardly growing septum primum has fused, and the primary foramen ovale has become reduced to the narrow transverse canal clearly seen in this model (Pl. XI. figs. 36 & 44, F.O.I.). Our observations on the A-V endocardiac cushions are in essential agreement with those of Born.

The bulbar cushions have undergone further development, but their detailed relations will not be described in this paper. It need only be noted that all the

four distal cushions are now present, and in the most distal part of the bulbus, distal cushions 1 and 3 have met so as to separate the ventral pulmonary, from the dorsal aortic channel, At the distal extremity of the bulbus these channels are continued as separate vessels.

The proximal bulbar cushions A and B extend into the right ventricle. Cushion A continues on to join the endocardiac cushion on the lateral side of the right A-V opening, whilst cushion B continues along the right edge of the interventricular septum and joins the fused endocardiac mass situated between the A-V openings, the point of junction lying at the left border of the right A-V opening. The prolongation of cushion A is much wider than that of B. The interventricular opening is thus surrounded by an oblique ring of endocardiac tissue, which is continuous cranially with the endocardiac tissue round the remains of the primary foramen ovale.

A-V bundle.—This makes its first definite appearance in the embryo of G.L. 8·5 mm., and is well marked in the present stage (Pl. XI. figs. 35, 35, & 44, A.V.B.). It appears as a darkly-stained cord of concentrically arranged cells situated in the thickened margin of the septum primum and surrounded by a narrow zone of loosely arranged tissue similar to that of the endocardiac cushions. In the present stage it can be followed dorsally from the septum primum, along the medial side of the caudal end of the sinu-atrial opening to terminate immediately under the endocardiac lining of the dorsal wall of the sinus in proximity to the opening of the inferior vena cava. From the septum it is traceable cranially for a short distance, just above the interventricular opening, and gradually decreases in size until it disappears. Whether the bundle arises *in situ*, as seems likely, or grows from one centre can only be determined by further investigation.

Summary.

A resumé of the tubular stage has already been given on pp. 764–7.

In the transition from the tubular to the definitive stage of the heart, two important events have taken place: (1) The division of the hitherto undifferentiated sinu-atrial cavity into sinus venosus and atrium, and (2) the division of the latter cavity into right and left atria.

In Model V. (Pl. VII. figs. 25, 26) the sinu-atrial region has grown considerably to form a large thin-walled cavity, its myocardiac and endocardiac layers being in contact with each other. The ventricles are in the form of a U-shaped tube; the left limb of the U is continuous with the sinu-atrial cavity by a constricted piece situated in a horizontal plane, the forerunner of the atrial canal. The right limb of the U passes into the bulbus, which runs in a dorsal direction. This phase of development has been observed in the 9-day embryos with between 20 and 30 somites.

During this phase a crescentic fold appears on the left lateral side of the caudo-dorsal corner of the sinu-atrial cavity; this is the beginning of the separation of the sinus from the atrium. Concurrently with the appearance of the fold, the left umbilical and omphalomesenteric veins begin to diminish in size.

In Model VI. (Pl. VIII. figs. 27, 28) the division of the sinu-atrial cavity into sinus and atrium is nearly completed, and the division of the latter into right and left atria has begun.

The sinu-atrial junction is now marked by a well-defined opening on the right side of the middle line; the left umbilical and omphalomesenteric veins have greatly diminished in size, while the corresponding right veins have increased.

The commencing division of the atrium into right and left chambers is initiated by the appearance of the septum primum. In Model VI. the septum is represented by an infolding in the sagittal plane, extending over the dorsal, cranial, and ventral walls of the atrium. The cranial and ventral parts of the infolding correspond to

the depression caused by the lodgment of the bulbus. The dorsal part is in a line with the attachment of the dorsal mesocardium, which is now present in the sinus region only.

With the appearance of the septum primum, the two atria begin to increase in size. The left increases by simple expansion of its wall, whilst the right increases partly by simple expansion, and partly by the addition of two accessory cavities, one larger than the other, in a localized thickening of the myocardium in the region of the right sinu-atrial junction.

The medial walls of these accessory cavities break down and the cavities become incorporated in the rest of the atrium, but the floor of the first cavity persists and becomes the septum spurium. This peculiar development of the right atrium has been observed in all the 11-day and the early 12-day embryos examined, and has been discussed in detail under Model VIII.

In Model VII. the atria have undergone rotation, so that they now lie cranially to the ventricles. The rotation has taken place around a transverse axis passing through the atrial opening of the atrial canal.

The sinus venosus reaches its maximum size in the stage of Model VI. when the differentiation of the sinu-atrial region is nearly completed. The right horn is larger and more cranial than the left. In the stage of Model VIII. (11 days), the sinus begins to diminish in size, and the two horns lie on the same level. In the last Model (XI.) the sinus is greatly reduced in size, and has receded to a position dorso-caudal to the atria.

The sinu-atrial opening at its first appearance in Model VI. is large and more or less circular in outline, and occupies practically all the floor of the right atrium. It is encircled over the greater part of its periphery by the right and left venous valves. The right lies caudal and ventral to the left. In later stages the opening becomes first oval, then slit-like in shape, and its position gradually changes till it becomes more or less sagittal and caudal in relation to the atrium. The two valves thin out, and in the last model come to occupy a right and a left position in relation to the opening, thus having completed their rotation. The left valve was originally cranial and on the right, and the right valve caudo-medial and on the left (in Model VIII.).

After the completion of the right atrium in the stage of Model IX. its wall begins to thicken and to develop trabeculæ; the septum spurium reaches its cranial limit and is marked by a sulcus on the surface. In the left atrium the pulmonary vein opens at the root of the septum primum, midway between its dorsal and ventral attachment.

The septum primum makes its first appearance in the stage of Model VI. It extends caudally as a median partition between the cranial parts of the two atria, its free border forming the cranial boundary of the primary foramen ovale. In the last model the foramen has become reduced to a narrow channel surrounded by endocardiac tissue.

The secondary foramen appears first in the stage of Model X. in the cranio-dorsal attachment of the septum primum. Also at the same time, the septum secundum appears as a thickening, on the right side the attachment of the septum primum. In the last model (Pl. XI. fig. 44) the secondary foramen is a large oval opening, the primary foramen is reduced to a narrow transverse channel, and the septum secundum appears as a well-marked flap lying on the right side of, and diverging from, the septum primum.

In Models V. and VI. the two ventricles are separated from each other by the left bulbo-ventricular sulcus, their caudal ends being joined together by a transverse segment. In Model VII. the interventricular sulcus makes its first appearance and is confined to the ventral surface. In later stages the sulcus extends in horse-shoe fashion—*i. e.*, ventrally, caudally, and dorsally. This sulcus corresponds to an infolding of the myocardium, forming the interventricular

septum. In Model X. the interventricular opening is circular in form and lies cranial to the septum. It is obliterated in the last stage by endocardiac tissue.

The bulbus in the early stage (Model V.) bends dorsally. It gradually straightens and rotates with the right ventricle to the ventral aspect of the heart. As the right ventricle extends cranially, the bulbus becomes shorter and less distinguishable from it on the external surface.

The endocardiac cushions make their first appearance in Model VII. The atrio-ventricular cushions appear as two pads, respectively dorsal and ventral to the A-V opening. The bulbar cushion appears as a horse-shoe-shaped band on the right side of the bulbus.

The two atrio-ventricular pads join at their ends in Model X., then medially in Model XI.; in so doing they surround the right and the left atrio-ventricular openings on both sides, and fill up the primary foramen ovale in the middle.

The bulbar cushion divides into two bands. These extend caudally into the right ventricle, and in so doing undergo a spiral twist, so that when they reach the ventricle the right band (A) becomes right-dorsal and the left band (B) becomes left-ventral in position. The former joins the right end of the cushion surrounding the right A-V opening, and the latter runs along the free border of the interventricular septum to reach the median mass of endocardiac tissue situated between the two A-V openings. The cranial parts of the bulbar bands in Model XI. are right and left in position, and constitute distal bulbar cushions 1 and 3 respectively. From the right (1) distal bulbar cushion (4) arises, and from the left (3) distal bulbar cushion (2).

Conclusions.

My observations would appear to support the following conclusions:—

(1) The caudal constriction forms the caudal limit of the heart primordium; a similar constriction forms the cranial limit. Between these two constrictions all the parts of the heart are developed, with the exception of the sinus venosus, which forms in large part from the cranial end of the right vitelline vein.

(2) Each half of the adult mammalian heart arises from the cardiac tube of the corresponding side—*i. e.*, the left atrium, the left ventricle, and the intrapericardial part of the aorta arise from the left cardiac tube, and the right atrium, the right ventricle, and the intrapericardial part of the pulmonary artery arise from the right cardiac tube.

I wish to thank Mr. A. K. Maxwell for the drawings of the models, and Mr. F. J. Pittock for the photomicrographs appearing in this paper.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Model I., myocardiac tubes (R 273, 8 days 20 hrs., 10 somites).
2. Model I. *a*, endocardiac tubes (R 273, 8 days 20 hrs., 10 somites).
3. Model II., myocardiac mantle (R 280 D, 8 days 20 hrs., 11 somites).

Plate II.

Fig. 4. Model II. *a*, endocardiac tubes (R 280 D, 8 days 20 hrs., 11 somites).
5. Model III., myocardiac mantle (R 278A, 8 days 20 hrs., 12 somites).
7. Model III. *a*, endocardiac tubes (R 278 A, 8 days 20 hrs., 12 somites).

PLATE III.

Fig. 6. Model III., left lateral view.
8. Model III. *a*, left lateral view.
9. Model III. *a*, right lateral view.

PLATE IV.

Fig. 10. Model IV., myocardiac mantle (R 200, 9 days, 13 somites).
11. Model IV. *a*, endocardiac tubes (R 200, 9 days, 13 somites).
13. Model IV. *a*, caudal view.

PLATE V.

Fig. 14. Photomicrograph of section (sl. 1, 5, 8) from Model I.
15. „ „ (sl. 2, 2, 3) „ „ II.
16. „ „ (sl. 2, 2, 10) „ „ II.
17. „ „ (sl. 2, 2, 13) „ „ II.
18. „ „ (sl. 2, 5, 4) „ „ II.

PLATE VI.

Fig. 19. Photomicrograph of section (sl 2, 5,|8) from Model III.
20. „ „ (sl. 3, 1, 5) „ „ III.
21. „ „ (sl. 3, 3, 9) „ „ III.
22. „ „ (sl. 2, 3, 10) „ „ IV.
23. „ „ (sl. 2, 4, 5) „ „ IV.

PLATE VII.

Fig. 25. Model V., ventral view (R 253, 9 days 10 hrs., 21 somites).
26. Model V., dorsal view.

PLATE VIII.

Fig. 27. Model VI., ventral view (R 275, 10 days 18 hrs., 34 somites).
28. Model VI., right lateral view.

PLATE IX.

Fig. 29. Model VI., view of cavity.
30. Model VII., ventral view (R 6, 11 days, 39 somites).
31. Model X., ventral view (R 5/20, G.L. 7·5 mm.).
32. Model XI., ventral view (R *a*, G.L. 10 mm.).

PLATE X.

Fig. 33. Sectional view of Model X.
34. „ „ „ „
37. Photomicrograph of section (sl. 4, 2, 3) from R 254, 9 days 10 hrs.
38. „ „ (sl. 4, 4, 11) „ Model VI.
39. „ „ (sl. 3, 3, 1) „ R 215, 10 days.
43. „ „ (sl. 6, 4, 8) „ Model X.

(Figs. 33–36 are reproduced from figures prepared under the direction of Prof. J. P. Hill.)

PLATE XI.

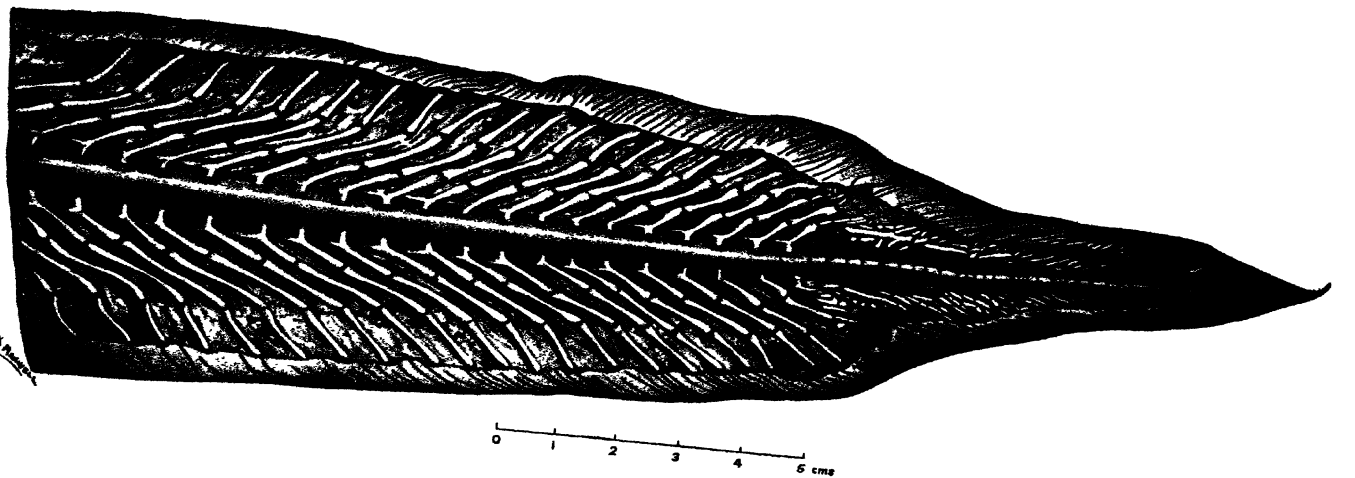
Fig. 35. Sectional view of Model XI.
36. „ „ „ „
40. Photomicrograph of section (sl. 2, 6, 13) from Model VII.
41. „ „ „ (sl. 3, 1, 15) „ Model VII.
42. „ „ „ (sl. 4. 5, 14) „ Model IX. (R 5–20, G.L. 7 mm.).
44. „ „ „ (sl. 10, 2, 8) „ Model XI.

Abbreviations.

A.A. = Aortic arch.
A.C.I = First accessory cavity.
A.C.II. = Second accessory cavity.
Atr = Atrium.
Atr.C. = Atrial canal.
Atr.C.G. = Groove of atrial canal.
A.P. = Anterior intestinal portal.
A-V.B. = Atrio-ventricular bundle.
B.C. = Bulbus cordis.
B-V.S. = Bulbo-ventricular sulcus.
Cr.C. = Cranial constriction.
Cd.C. = Caudal constriction.
D.C. = Duct of Cuvier.
D.M. = Dorsal mesocardium.
E.C. = Endocardiac cushion.
E.L.T. = Enlargement of caudal end of left tube.
E.T. = Endocardiac tube.
F.G. = Fore-gut.
F.O.I. = Primary foramen ovale.
F.O.II. = Secondary foramen ovale.
G.L.T. = Groove between atrium and sinus region of left tube.
I.S. = Intertubular sulcus.
I.S.R. = Intertubular sulcus and ridge.
I V.C. = Inferior vena cava.
I.V.S. = Interventricular sulcus.
I.V.Sp. = Interventricular septum.
M.C.P. = Middle cardiac plate.
M.T. = Myocardiac tube.
O.V. = Omphalomesenteric vein.
P.S. = Pars interseptale.
S.I. = Septum primum.
S.II. = Septum secundum.
S.A.C. = Sinu-atrial cavity.
S.A.J. = Sinu-atrial junction.
S.A.O. = Sinu-atrial opening.
S.A.R. = Sinu-atrial region.
S.Sp. = Septum spurium.
S.Tr. = Septum transversum.
S.V. = Sinus venosus.
T.Gr. = Transverse groove on bulbus.
U.V. = Umbilical vein.
V. = Ventricle.
Vt.V. = Vitelline vein.
Vt V.Cr. = Cranial end of vitelline vein.
V.Vl.R. & V.Vl.L. Right and left venous valves.
(R) = Right.
(L) = Left.

Bibliography.

1. Born, G. 1889. Beiträge zur Entwicklungsgeschichte des Säugethierherzens. Archiv für mikroskop. Anatomie, Band xxxiii.
2. Davis, C. L. 1927. Development of the Human Heart from its First Appearance to the Stage in Embryos of Twenty Paired Somites. Carnegie Contributions to Embryology, No. 107.
3. Murray, Henry A., Jr. 1919. The Development of the Cardiac Loop in the Rabbit, with especial reference to the Bulboventricular Groove and Origin of the Interventricular Septum. Amer. Journ. of Anatomy, vol. xxvi.
4. Parker, Katharine M. 1915. The early Development of the Heart and Anterior Vessels in Marsupials, with special reference to *Perameles*. Proc. Zool. Soc. London, 1915.
5. Schulte, H. von W. 1915. The Fusion of the Cardiac Anlages and the Formation of the Cardiac Loop in the Cat. Amer. Journ. of Anatomy, vol. xx.
6. Tandler, J. 1912. The Development of the Heart. Keibel & Mall, Manual of Embryology.
7. Tandler, J. 1913. Anatomie des Herzens (in Bardeleben, Handbuch der Anatomie), G. Fischer, Jena.
8. Wang, C. C. 1917–18. The Earliest Stages of the Development of the Blood-vessels and Heart in Ferret Embryos. Journ. of Anat. vol. lii.
9. Waterston, D. 1918. The Development of the Human Heart. Trans. Roy. Soc. Edin. vol. lii. part 2.
10. Watson, Katharine M. 1924. The Origin of the Heart and Blood-vessels in *Felis domestica*. Journ. of Anat. vol. lviii. part 2.
11. Yoshinaga, A. 1921. A Contribution to the Early Development of the Heart in Mammalia, with special reference to the Guinea-pig. Anat. Record, vol. xxi.



TAIL OF ADULT LEPIDOSIREN PARADOXA DISSECTED TO SHOW VERTEBRAL COLUMN AND CARTILAGE BLOCKS.

John Bale, Sons & Danielsson, Ltd. London.

35. Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*.

By AGNES E. MILLER, M.A.*, University of Glasgow.

[Received May 5, 1930: Read June 3, 1930.]

(Plate I.†; Text-figures 1–5.)

A well-known and interesting characteristic of modern Dipnoan fishes is the presence in the tail region of a number of blocks of cartilage presenting a superficial resemblance to vertebral centra, which are otherwise conspicuous by their absence in that group. The purpose of this note is to make known the main results of a detailed examination of the structures in question as they occur in the South American Lungfish, *Lepidosiren paradoxa*.

The typical adult condition is shown in Plate I., where the notochord enclosed in its cartilaginous secondary sheath is seen to be continued towards the tip of the tail by a series of thirty-six cartilaginous blocks closely resembling typical vertebral centra. The number of such blocks shows great differences in different individuals, and it is impossible to decide upon any particular number as being "normal," owing to the fact that the tip of the tail, and indeed the tail region generally, is exceedingly liable to damage, and has in the great majority of specimens been secondarily shortened by disease or other injury.

The question now presents itself—Is the resemblance of the blocks of cartilage to vertebral centra merely superficial, or is it fundamental? The importance of this question will be recognized when it is recalled that every zoological text-book gives us one of the main Dipnoan characteristics that their axial skeleton is devoid of centra.

The obvious course is to turn to the evidence of embryology for the answer. In text-fig. 1, a reconstruction drawing from a young *Lepidosiren* of stage 37, there are present in all twenty-four blocks of cartilage, extending from the end of the notochord to the tip of the tail.

From the next illustration (text-fig. 2), which shows the hind end of the notochord and the first of these cartilage blocks, it is obvious that the entire series of cartilage blocks lies quite outside the notochordal sheath. The notochord itself comes to an abrupt end, and the primary sheath is to be observed terminating in the substance of the first cartilage block of the series.

In this particular section the cells of the notochord have shrunk away somewhat from the primary sheath, which nevertheless is obviously vanishing off in the substance of the first of these cartilage blocks.

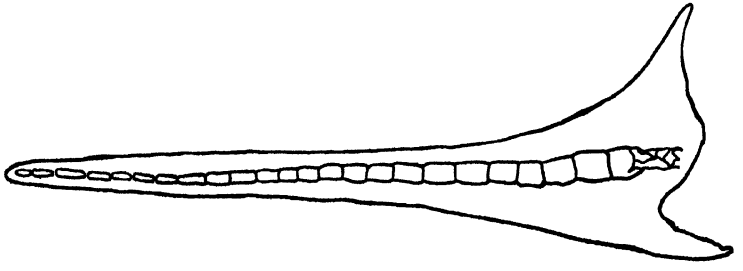
Text-fig. 3, a section through the tail of a young *Protopterus* of 96 mm., makes quite clear the fact that the cartilage of the secondary sheath is continuous with that of the first cartilage block of the series.

The possibility that these cartilaginous centra are not normal, but due to regeneration, is naturally suggested by the appearance of such sections (*cf.* also Plate I.), and it is not lightly to be dismissed. It should be said, however, that although the tip of the tail is exceedingly liable to injury during the life of the *Lepidosiren*, examination of large numbers of individuals of early stages from about stage 32 onwards has failed to disclose a single one in which the segmental

* Communicated by Prof. J. GRAHAM KERR, F.R.S., F.Z.S.

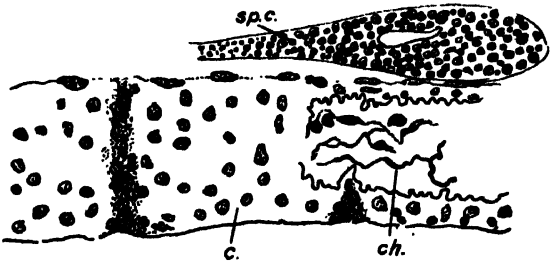
† For explanation of the Plate, see p. 789.

Text-figure 1.



Reconstruction of tail of *Lepidosiren* larva of stage 37, with twenty-four cartilage blocks.

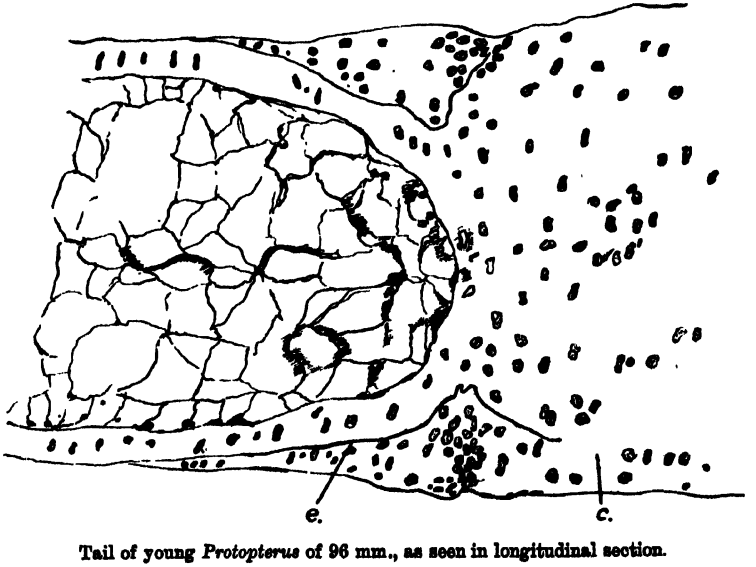
Text-figure 2.



Lepidosiren larva of stage 37. End of notochord as seen in longitudinal section under high power (oc. 2, Zeiss D).

c, first cartilage block of series; *ch.*, notochord; *sp.c.*, spinal cord.

Text-figure 3.



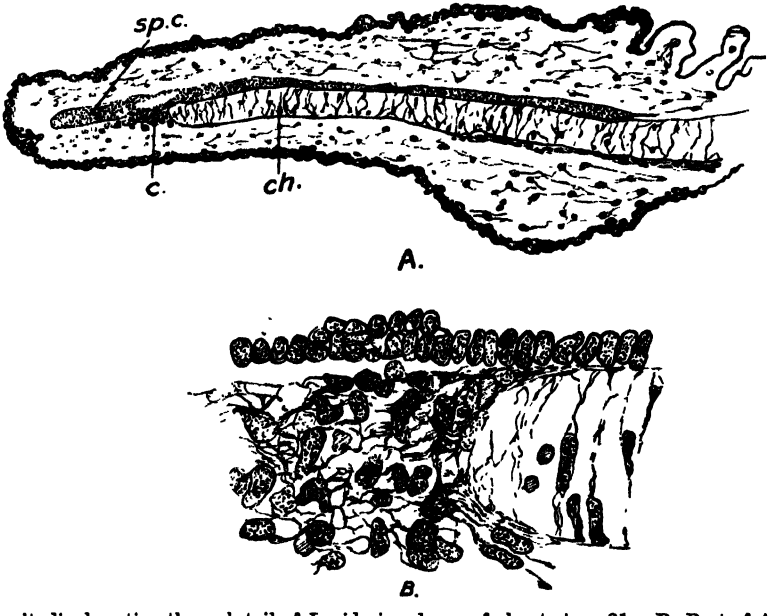
Tail of young *Protopterus* of 96 mm., as seen in longitudinal section.

c., first cartilage block of the series; *e.*, primary sheath of the notochord.

blocks of cartilage were absent. The really important point is that here in the tail region of those Lungfish we have present an innate tendency towards the production of segmentally arranged blocks of cartilage; the question whether injury followed by regeneration is normally required for this tendency to find full expression would, even if answered in the affirmative, be of minor though still considerable interest. In this connection it is worth recalling that the young *Lepidosiren* of stage 32 have not yet reached a condition of development when they are capable of biting, so that the risk of such injury between stage 32, when cartilage blocks are first quite definitely to be observed, and stage 38, when the jaws are sufficiently developed to enable the creature to feed, is considerably lessened.

So far as my investigations go, there are no definite cartilage blocks present

Text-figure 4.



A. Longitudinal section through tail of *Lepidosiren* larva of about stage 31. B. Part of A more highly magnified, showing connective tissue becoming converted into cartilage.

(Letters as on previous text-figures.)

before stage 31, although at this stage it is becoming obvious that the connective-tissue cells at the end of the notochord are becoming converted into cartilage (text-fig. 4).

It has been stated by Gadow that the notochord of the Dipnoi is potentially chordo-centrous on account of the fact that the chordal sheath is partly cartilaginous, and in spite of the fact that it shows no trace of division into vertebræ. It seems, however, that the conception of a centrum derived entirely from the chordal sheath is somewhat hypothetical, since not only is the chondrification of the secondary sheath affected by the immigrant cells from the cartilaginous arch elements which have broken through the primary sheath, but in the case of Elasmobranchs the spreading bases of the arch elements come to envelop the whole notochord with its sheaths in a layer of external cartilage. While in early

stages the primary sheath forms a distinct boundary between the two layers of cartilage—of sheath and arch origin respectively—this tends to disappear later, and it becomes quite impossible to say where the one ends and the other begins. Further, the general facts of comparative embryology impress upon us the very much greater evolutionary importance of the arch centrum as compared with the sheath centrum.

The general impression borne in upon me by my study of these blocks of cartilage in the Dipnoan tail is that we are not justified in refusing to them the term "vertebral centra," and that in consequence we should define Dipnoi not as fish without vertebral centra, but rather as fish in which there are present vertebral centra only towards the tip of the caudal region.

If we consider the presence of these centra from the point of view of evolution, we cannot but remember that the normal condition is for the vertebral column to be homogeneous from end to end. This at once raises the question as to whether the segmentation of the vertebral column towards the posterior end of the Dipnoan body is an incipient stage in the segmentation of the axial skeleton, or whether it is the last remnant of a segmentation which once extended throughout the body. This morphological problem must be kept in relation to physiological considerations. In the living Dipnoan the creature still retains the primitive vertebrate method of progression by passing waves of lateral flexure back along the length of the body, so that there is in these animals, so far as surviving members of the group are concerned, none of that concentration of propulsive force at the hinder tip of the body which finds its expression in a spread-out caudal fin.

This consideration renders it improbable that the tail region of the Dipnoi is in any active condition of forward evolution; and indeed the probability lies in quite the opposite direction, namely that the terminal region of the body is of no functional significance, and therefore degenerative. One may recall the apparently meaningless growth in length which often takes place in the young Dipnoan, as for example in the young *Protopterus*, where the tail region may grow out into a filament as long as the body. The tendency towards segmentation, which becomes visible in the Dipnoan in this terminal part of the tail free from adaptive necessity, seems to fit in most easily with the hypothesis that here we have the last vestige of a once segmented condition of the vertebral column as a whole. The paucity of corroborative evidence from the side of palæontology ceases to be a formidable difficulty when we bear in mind, firstly, that uncalcified cartilaginous centra are in the highest degree perishable, and, secondly, that the vertebral column of ancient Dipnoans is so generally concealed in a body the outer layer of which consists of a thick coating of calcified scales.

The possibility that a completely segmented vertebral column may have been the condition in the ancestral forms of the modern Dipnoi would have an interesting bearing upon the problem of the affinities to this group of that much discussed fossil enigma, *Palæospondylus gunni*.

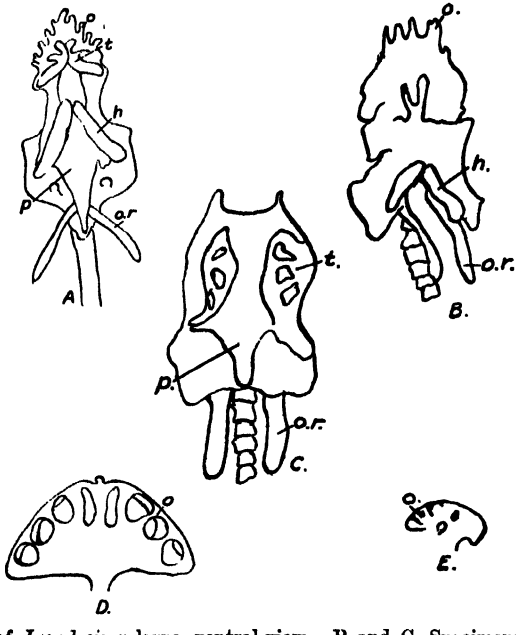
To the opinion still held by various palæontologists, following Traquair, its original describer, that this creature is to be classed as a Devonian representative of the Cyclostomata, there are several objections, one of the most serious being that *Palæospondylus* shows a completely segmented and apparently chordo-centrous vertebral column.

Professor Graham Kerr, in pointing out many years ago that the affinities of this creature were strongly Dipnoan, found the most important argument against this view in the fact that *Palæospondylus* possessed definite vertebral centra.

It may be recalled that *Palæospondylus* was first described by Traquair in the 'Annals and Magazine of Natural History,' ser. 6, vol. vi., having been got from the Achanarras quarry, near Thurso. This great authority on the palæontology of fishes concluded that it was a "primitive lamprey." Professor Kerr, as a member

of the Royal Physical Society and a personal friend of Traquair, was particularly interested in *Palæospondylus*, and had the main facts of its structure clearly in mind during his second *Lepidosiren* expedition, 1896–97. While on that expedition it happened that a particular batch of small *Lepidosiren* larvæ were dead when brought in and were just put on one side; by next morning the specimens were completely macerated and, on pouring away the water, there were found merely skeletal remains. In such specimens the limbs and limb-girdles being free from the axial skeleton had naturally disappeared, and the same applied to the massive lower jaw, which drops off, along with, as a rule, the branchial arches, at an early stage of maceration; in addition, the bars of the olfactory capsules were commonly frayed out into little tags projecting from the front end

Text-figure 5.



A. Macerated skull of *Lepidosiren* larva, ventral view. B and C. Specimens of *Palæospondylus*, after Traquair. D. Dorsal view of olfactory capsule of *Lepidosiren* larva. E. Front end of skull of *Palæospondylus*, after Bashford Dean.

h., hyoid; *o.*, olfactory capsule; *o.r.*, occipital rib; *p.*, parasphenoid; *t.*, tooth-plates.

of the skull (text-fig. 5, A, *o*). The appearance of *Lepidosiren* skeletons in this condition suggested irresistibly those of so many specimens of *Palæospondylus*. Professor Kerr, after his many years of research upon the morphology of the Dipnoi and other lower vertebrates, adheres to the opinion that it is quite unjustifiable to hold that *Palæospondylus* is anything else than a member of that group of primitive fishes to which we apply the name Dipnoi.

In estimating what weight is to be attached to this opinion, we cannot ignore the fact that its protagonist is probably the only living morphologist who has had the opportunity of examining large numbers of small Dipnoan skeletons in that macerated condition, which provides the usual material for fossil remains.

On account of the great interest taken by palæontologists in *Palæonspondylus*, I will summarise shortly the interpretation of its representations by Traquair that would be given by one familiar with Dipnoan embryology. I confine myself naturally to the representations of actual individual specimens and ignore figures expressing theoretical interpretations.

In text-fig. 5 there are reproduced in outline (B and C) Traquair's figures of two of his most perfect specimens, and alongside (A) I give an outline of what appear to be the corresponding structures in *Lepidosiren* as shown by the macerated skeleton of a young specimen. To facilitate comparison I have made the text-figures of approximately the same size, although in actual fact *Palæospondylus* is much smaller.

Two bones (text-fig. 5, B; *h.*) correspond in position, shape, and relative size to the hyoid arch of *Lepidosiren*; of this one feels more particularly assured by Dr. Traquair's statement that we are viewing the ventral surface of the skull of *Palæospondylus*. In the second specimen (C) there is again a structure showing strong resemblance in shape, position, and relative size to the parasphenoid bone (*p.*) of *Lepidosiren*; while marks further forward recall the characteristic tooth-plates (*t.*) of the Dipnoi.

The tags ("cirri" of Traquair) seen projecting from the front end of many specimens of *Palæospondylus* (*o.*) are represented in the macerated *Lepidosiren* by the remains of the cartilaginous trabeculæ of the olfactory capsule; and in this connection it is of interest to observe that Bashford Dean figures a specimen of *Palæospondylus* (text-fig. 5, E) in which the front end of the head skeleton is limited by a curved bar. The figure of the front end of a *Lepidosiren* larva head (text-fig. 5, D) shows how closely this agrees with the cartilaginous support of the olfactory capsule before it becomes frayed out in the process of maceration. Perhaps the most characteristic single feature of *Palæospondylus* is the pair of elongated structures (*o.r.*) attached to the skull one on each side posteriorly. The Dipnoi alone amongst vertebrates are characterised by a pair of elongated bones (*o.r.*) attached to the skull, one on each side posteriorly—the enlarged ribs of the occipital vertebra, which has become fused with the cranium. Graham Kerr homologises these *Palæospondylus* structures with those occipital ribs—a possibility which is also contemplated by Bashford Dean.

W. J. and I. Sollas believe the structures in question to be attached to the "last branchial arch." One is justified, however, in being somewhat sceptical as to this, owing to the liability to error inherent in the wax-plate method of reconstruction, more especially when applied to the macerated and crushed remains of fossil organisms. Even if the Sollases were correct as to the attachment of these rods to a branchial arch, they might quite possibly represent the skeletal support of external gills, such as are to be seen in an incipient or a vestigial form in the external gill of a young *Polypterus*, for external gills are known to exist in the larvæ of two of the three living Dipnoi; and now that we know more regarding the morphology and development of external gills, there seems every reason for regarding them as archaic organs and by no means modern adaptations.

Enough has, I think, been said to bring out the strong resemblances between the skeleton of *Palæospondylus* and that of the modern Lungfish, and to justify of us in the belief that *Palæospondylus* was simply a small-sized Dipnoan.

The most conspicuous difficulty in the way to this conclusion is, as already indicated, the completely segmented vertebral column of *Palæospondylus*; but even that difficulty, such as it is, would be removed if we accept the view supported in this note that the blocks of cartilage in the tail of the modern Lungfish are to be regarded as a vestige or a reminiscence of an earlier segmented condition of the whole vertebral column.

Literature.

Agar, W. E. Development of Skull and Visceral Arches in *Lepidosiren* and *Protopterus*. Trans. Roy. Soc. Edin. vol. xlv. pt. 1, no. 3, 1905.

Brindley, H. H. Note on some Abnormalities of the Limbs and Tail of Dipnoan Fishes. Pub. Phil. Soc. Camb. vol. x. 1900.

Dean, Bashford. Affinities of *Palæospondylus*. Proc. Zool. Soc. London, 1898.

——— Devonian Lamprey. New York Ac. of Sc. vol. ii. pt. 1, 1900.

——— Further Memoir on *Palæospondylus*. Science, n. s. vol. xix. no. 480, 1904.

Gadow, H. Evolution of Vertebral Column of Fishes. Phil. Trans. Roy. Soc. vol. clxxxvi. 1894.

Günther, A. *Ceratodus*. Phil. Trans. Roy. Soc. 1871.

Holmgren, N. Some Observations about the Growth of the Tail in *Lepidosiren*. Acta Zool. vol. ix. 1928.

Kerr, J. Graham. Keibels Normentafeln Entw. Wirb., Heft x. Jena, 1909.

——— The Zoological Position of *Palæospondylus gunni*. Pub. Phil. Soc. Camb. vol. x. pt. 5, 1900.

——— Text-book of Embryology.—Vol. II. Vertebrata. London, 1919.

Kisslewa, S. Skelett von *Lepidosiren*. Bull. Soc. Natur. Moscow, 1928.

Sollas, W. J. & I. An Account of the Devonian Fish *Palæospondylus gunni*. Phil. Trans. Roy. Soc. vol. cxcvi. 1903.

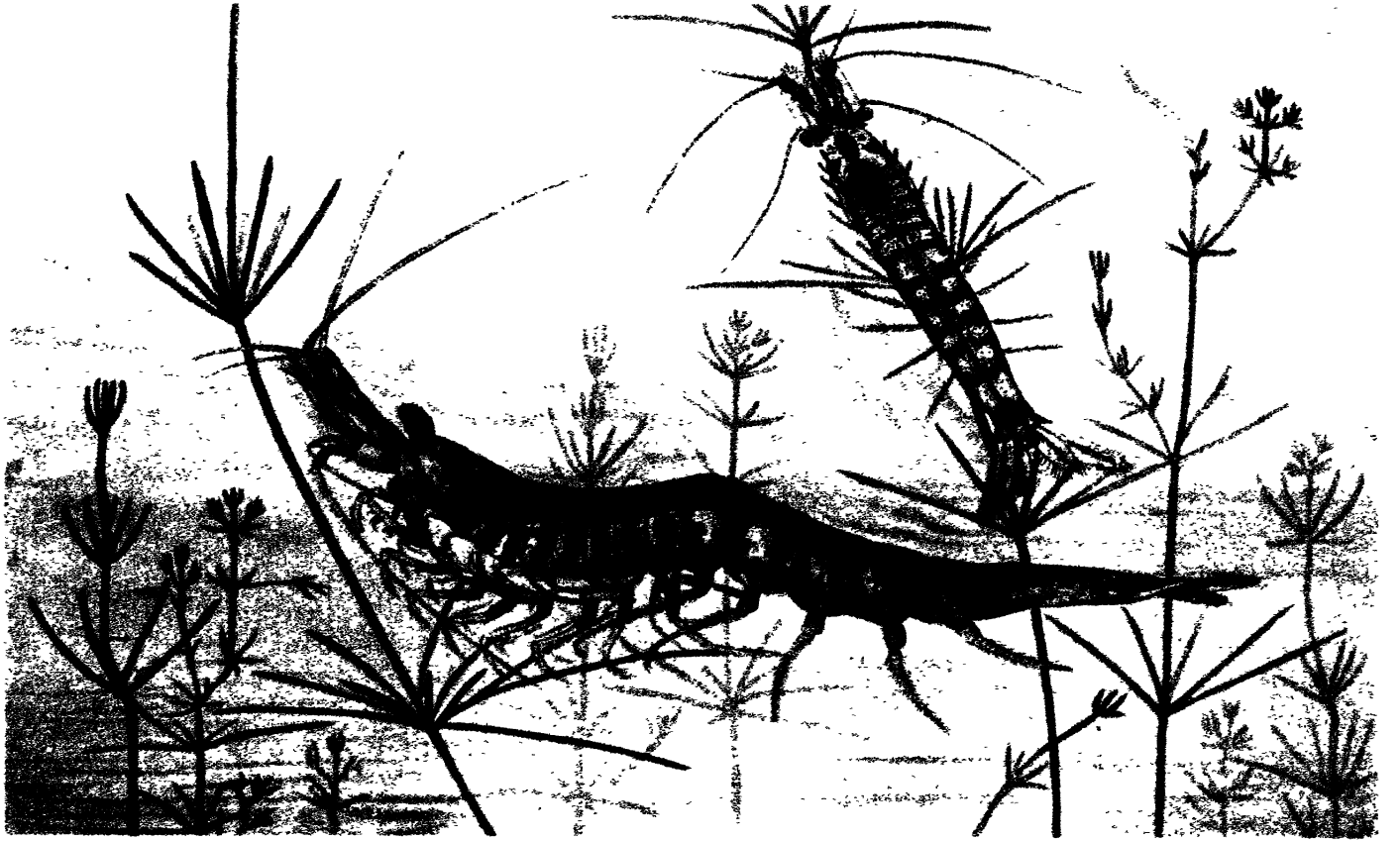
Traquair, R. H. On some Fossil Fishes. Ann. & Mag. Nat. Hist. ser. 6, vol. vi. 1890.

——— Further Description of *Palæospondylus gunni*. Proc. Roy. Phys. Soc. Edin. vol. xii. 1893.

——— Still Further Contributions to our Knowledge of *Palæospondylus gunni*. Proc. Roy. Phys. Soc. Edin. vol. xii. 1893.

EXPLANATION OF THE PLATE.

Tail of adult *Lepidosiren* dissected to show vertebral column and cartilage blocks.



The Half-Tone Engraving Co. Ltd., London.

IMMATURE AND ADULT *Paranaspides lacustris.*



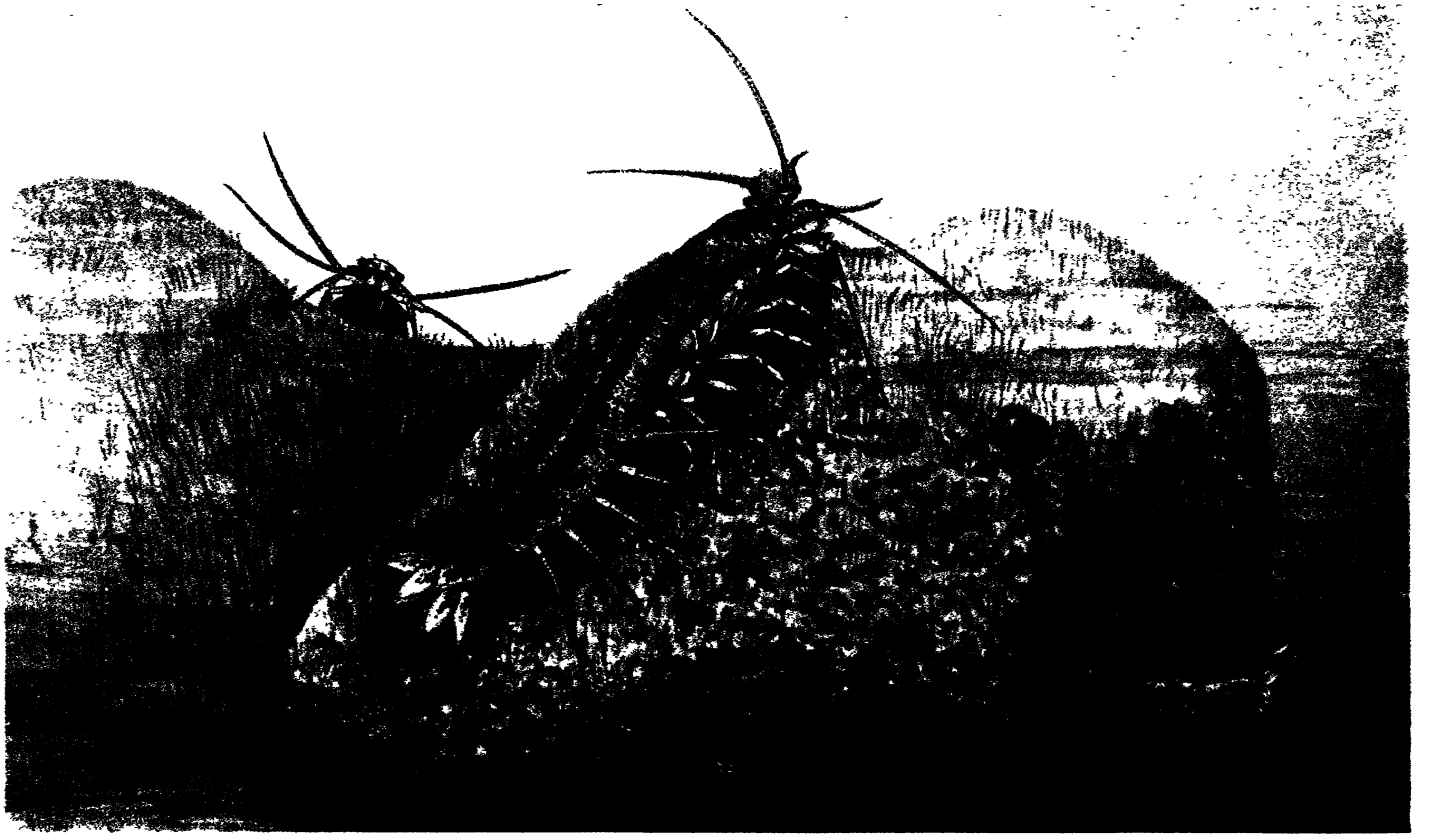
The Half Tone Engraving Co. Ltd., London

DORSAL VIEW OF DARK VARIETY OF *Anaspides tasmaniae*.



The Half-Tone Engraving Co Ltd London

LATERAL VIEW OF DARK VARIETY OF *Anaspides tasmaniae.*



The Half-Tone Engraving Co. Ltd., London.

LIGHT VARIETY OF *Anaspides tasmaniae.*

36. Notes on the Habits and Feeding Mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida).

By S. M. MANTON, M.A., Ph.D., F.L.S. (Demonstrator in Comparative Anatomy in the University of Cambridge and Fellow of Girton College) *.

[Received March 1, 1930: Read May 6, 1930.]

(Plates I–IV. †; Text-figure 1.)

INTRODUCTION.

A preliminary account of the probable methods of feeding of *Paranaspides*, *Anaspides*, and *Koonunga* and the structure of the limbs concerned has already been given (Cannon and Manton, 1929). These results were based on an examination of preserved material. In 1929, with assistance from the Balfour Fund, I was able to spend some time in Tasmania and examine *Paranaspides* in the Great Lake and *Anaspides* on Mount Wellington under natural conditions. My thanks are due to the Trustees of the Balfour Fund for enabling me to carry out this work, and to Professor Thomson Flynn for his never-falling assistance while I was working in Tasmania. The Hydro-electric Department of Hobart provided me with the use of their launch on the Great Lake, and through their assistance *Paranaspides*, now nearly extinct, was obtained.

HABITAT OF *PARANASPIDES*.

Paranaspides used to be found abundantly in the Great Lake of Tasmania situated at a height of 3700 feet and water-depth of about 20 feet. The littoral zone of the lake in many parts was clothed with a rich growth of weeds, and among the weeds *Paranaspides* could be found in plenty (Pl. I.). The Amphipod *Phreatoicus* was also abundant, and these two Crustacea were considerably preyed upon by the brown and rainbow trout which have been introduced into the lake. During the last few years a dam has been built across the southern outlet of the lake, raising the water-level of the lake by about 33 feet. The lake area has been much increased, but the shore-line is of about the same length owing to the obliteration of many bays and promontories. This alteration of water-level has had a profound effect on the biology of the lake. The sudden deepening of the water and drowning of the old shore-line resulted in the dying off of nearly all of the old weed-growth round the shores. The formation of new lake-bottom in the present littoral zone is a very slow process, and has as yet hardly begun. This zone is composed of dense uncleared gum-forest or rough country now covered with a few feet of water. Fresh weed-growth on the new banks of the lake has not yet begun, and weeds are now very scarce in the lake.

As the weeds disappeared so *Paranaspides* also became scarce, and in 1929 it had not been seen for several years. It could not be found at the south end of the lake, and was absent from the stomach-contents of trout caught in this region in January 1929. At the northern end of the lake a patch of weeds was found near the old shore-line over a region originally a few feet deep. Repeated trawling over these weeds with a small net secured one adult *Paranaspides* and several immature specimens. Trout caught in this part of the lake were said to be feeding partly upon *Paranaspides*.

* Communicated by L. A. BORRADAILE, M.A., F.Z.S.

† For explanation of the Plates, see p. 800.

Phreatoicus, unlike *Paranaspides*, has been able to accommodate itself completely to the changed conditions. It lives on the bottom mainly under stones, lying sideways against the surface of the stone. All round the new shores of the lake *Phreatoicus* is abundant, and in January 1929 appeared to be the only organism of any size present in large numbers near the shores, apart from planarians, which were common in places. In parts of the lake *Phreatoicus* appeared to form the bulk of the trout food when the fish were not feeding largely on caddis-fly.

Besides these changes in the littoral regions of the lake the open water has also been affected by the altered conditions. G. Smith reports (1909, p. 83) "that the amount of . . . plankton . . . is very small" in the Great Lake. The churning up of the bottom by storms over the shallow waters was suggested by Smith to be the cause of the scarcity of plankton. Now the lake supports an abundant plankton composed at the north end in January 1929 almost entirely of *Daphnia cariata*. This rich growth may have been induced by the supply of phosphates and other matter washed into the lake from the newly submerged banks.

As normal conditions become re-established in the lake, weeds will probably become less restricted. It is to be hoped that with the spreading of weeds *Paranaspides* will recolonise the lake and spread from its present restricted distribution.

Habits of *Paranaspides*.

When placed in aquaria provided with weeds from the lake, *Paranaspides* was usually to be found clinging to the weed in a shrimp-like manner with its thoracic legs, or to be gently swimming about among the weeds. It showed no tendency to leave the weeds, and immediately sought refuge among them if forcibly removed. When alarmed *Paranaspides* executes powerful and rapid jumps, and may even jump out of the water in a tank.

The immature animals show two colour varieties, one mainly green and the other brown. The single mature specimen was brown (Pl. 1.). The musculature and cuticle are transparent, as in many marine Mysids, and when the animals are quiet among weeds they become very inconspicuous. Doubtless both *Paranaspides* and *Phreatoicus* enjoy a certain amount of protection from predatory fish by the habit of living among weeds and under stones respectively.

Swimming is carried out mainly by the pleopods, which project more laterally than ventrally. During gentle swimming the rate of beat of the pleopods is about 120 times a minute. The thoracic exopodites project laterally and forwards, with the tips curled dorsally (Pl. 1.). They are continually in motion, but the beat is a simple antero-posterior swing, not a circular rotation as in a Mysid or Euphausid. The usual rate of beat of the exopodites is about 250–300 times a minute, and generally they beat independently of the pleopods, although occasionally exopodites and pleopods may beat in series with one another.

The feeding mechanism of *Paranaspides* is not utilized exactly in the manner previously suggested (Cannon and Manton, 1929). The maxillary filtering mechanism is described (Cannon and Manton, 1929, pp. 177–79), and it is operated just as in a Mysid. It is, however, largely unaided by a food-bearing stream of water from the thorax. As in a Mysid the mouth-parts are usually in rapid motion, and if an animal is placed in a suspension of starch-grains or iron saccharate, the stomach is speedily filled with these substances. Sections of an animal kept in an iron saccharate suspension show that the particles, rendered blue by treatment with ferrocyanide, take the same course through the mouth-parts to the oral cavity as in *Hemimysis*. The detailed movements of the mouth-parts resemble those of *Anaspides*, which will be considered fully below (p. 797).

It was suggested that the exopodites might produce swirls laterally as in *Hemimysis*, which would suck in food-bearing streams of water to the mid-ventral groove between the thoracic legs (Cannon and Manton, 1929, p. 179). However,

with the simple antero-posterior beat of the exopodites there is no tendency for water to be forced between the limbs as in a Mysid or Euphausid showing a rotatory beat of the exopodites. Stained starch-grains may be seen to flow slowly through the inter-limb spaces on either side and through the ventral groove between the limbs, but this takes place in either direction. During swimming the forwardly directed epipodites must direct some water into the inter-limb spaces, and the bases of the trunk-limbs also beat obliquely inwards and forwards. Thus it is possible that a feeble food-bearing current may be produced at times along the ventral groove. However, the efficient filtratory feeding is mainly due to the independent action of the maxillary filtering mechanism.

Besides filtering the surrounding water, *Paranaspides* also eats the slime, detritus, and diatoms covering the narrow stems of the weeds. This matter is mainly swept up by the broad setose flanges on the præischia of the first trunk-limbs. The whole limb vibrates, and the flanges from either side meet ventrally, shuffling across the other mouth-parts, which may be stationary if no food is being obtained. The soft particles so dislodged are swept between the distal setose endites of the maxilla and maxillule. The bases of the first trunk-limbs are held closely together, preventing backward escape of particles, which are then transferred to the mouth as in a Mysid. The stomach-contents of *Paranaspides* consisted of an unrecognizable mass of detritus, finely divided and containing numerous diatoms.

Habitat of *Anaspides*.

Anaspides occurs in all the streams and pools upon Mount Wellington which are provided with flowing water. The animals are present abundantly on the plateau on the top of the mountain and in the upper parts of the streams above 1400 feet, but can also be found at lower levels. On the plateau known as the "Plains" arise rivulets forming the source of the North West Bay River, and here *Anaspides* reaches its largest size. In this locality the animals are all dark in colour, an olive-green or dark brown (Pls. II. & III.). In the streams below the "Springs," such as in Fern Tree Bower Creek or S. Crispin's Well Creek, the animals are not so large at maturity and are all of a light brown colour (Pl. IV.).

The pools upon the "Plains" at a height of about 3600 feet are variable in appearance, and all those that are permanent are liable to harbour the mountain-shrimp. The eastern part of the Plains is hedged by higher ridges up to 4000 feet in height, forming the watershed. Rain collects in the basin-shaped plateau, forming bogs and transitory pools in the higher parts to the east. The boggy land drains away to the south-west, and is covered with permanent small pools of variable water-level. As the level of the Plains slopes gently downwards the pools empty into one another by short falls of a few inches, and definite springs make their appearance, giving origin to tumbling streams. The pools vary in size from 1–12 yards in length, and may be a few inches to 2–3 feet in depth. They are isolated from one another in summer, except for the water trickling from one to another through the soil and grasses. The temperature of the water in the upper pools varies with the weather conditions from 7°–14° C. during the daytime in the summer. The water in the stream never becomes so warm as in the shallow exposed pools. The whole region is under snow in the winter for 3–4 months.

The pools in the stream and above it are generally dark in colour, owing to the dark green weeds and moss richly overgrown with dull-coloured algæ and detritus in the upper pools, and partly to the usual rippling of the water surface by the wind. *Anaspides* is found abundantly in pools provided with a soft muddy bottom partly covered by plant-growth. Some of these pools appear a grey-green in colour, while others are covered with a red-brown deposit. *Anaspides* does not occur in pools devoid of plant-growth, and cannot usually be found where there is a clean, bright green, moss-covered bottom. In the main stream itself the plant-growth is

less dirty in appearance, but the rocks all bear an algal growth, and the mud-bottom is of similiar appearance.

Anaspides breeds in the main stream and in the bog-pools. During January and February adults up to 38 mm. and small forms 7–15 mm. in length could be found, but the smallest individuals were only present in the main stream, where the water is cooler. Possibly the breeding-season is later in the cooler water of the main stream.

In the streams flowing down the slopes of Mount Wellington the growth of weeds and moss over the bottom is usually considerably lighter in colour than in those on the top of the mountain, and in sheltered basins, with an undisturbed water surface and more abundant growth of filamentous algæ, the general coloration may be very light. Although the *Anaspides* in these streams are a light brown, they are very conspicuous against their even brighter background.

Habits of *Anaspides*.

Ideal conditions for observing the living animals in their natural state were found in the small semi-isolated pools on top of Mount Wellington, and in a favourable pool naturally stocked with about twelve large *Anaspides* and many smaller ones the animals could be observed at all times. Further, in these pools the animals appear unconscious of observation, while in streams and in more accessible places not only is it difficult to watch one individual for more than a few moments, but the animals are very shy. *Anaspides* were also kept in captivity in running water from a spring at a height of about 2150 feet quite successfully.

The degree of activity of the shrimps during the daytime is variable, but in captivity they are far more active at night than during the day. *Anaspides* reacts to moderate sunlight by taking a sunbath or foraging for food, but strong sunlight, especially if it heats the water to any extent, causes the animals to seek shelter under the banks or under tufts of moss and weed. A temperature of about 20° C. proves fatal if maintained for long, especially at night. During a dull day the animals may or may not be active, during captivity they usually remain hidden. The smallest individuals are active usually at all times, but confine their excursions to the surface of the algal-coated stones and weeds or moss. They do not seek to hide themselves nor do they wander or swim freely away from surfaces. The larger *Anaspides*, when active, spend most of their time walking or half swimming over the bottom. They seldom swim freely for far through the water, unless to reach another rock- or weed-surface, or unless they have been frightened. Never have I observed a healthy *Anaspides* swimming on its back, as stated by Smith (1908, p. 466). This point has received particular attention, and I am certain that only a sick and dying *Anaspides* swims thus. The animal may momentarily get into this position when crawling over or looking for weed at the surface, but when freely swimming it at once rights itself.

Swimming and walking movements.—Both in swimming and walking *Anaspides* uses the thorax and abdomen as a single functional region. In walking the second to eighth thoracic legs are used, and frequently the five pairs of pleopods when the surface is uneven. The pleopods project almost laterally, not ventrally, as is usual in the Malacostraca (Pl. II.). The thoracic endopodites project outwards, with the distal parts strongly flexed ventrally. The legs are successively moved from behind forwards. When the pleopods are used for walking they move in series with the thoracic endopodites, and are used mainly in walking over rough surfaces of weed and moss. The tips of the pleopods bend in contact with the substratum, and help push the animal along. The anterior three pairs of pleopods are used more frequently than all five pairs in this manner. Those not being used project laterally and remain stationary.

In swimming the pleopods are used exactly as in walking, only they do not touch the ground. The metachronial rhythm is seen in the photograph.

The thoracic exopodites are continually in motion, and resemble those of *Paranaspides* in position. The beat also is a simple antero-posterior swing. Occasionally the tips of the posterior exopodites show a flattened elliptic path, but the course of the exopodite when beating slowly is not always regular. The frequency of the beat in the adult is only about 100 times a minute when the animal is at rest, and about 200 times a minute in young individuals. This is much slower than in filter-feeding Mysids and Euphausids. When swimming the pleopods, unlike those of most Malacostraca, beat in series with the thoracic exopodites. When stationary the first one or two pairs of pleopods beat gently in series with the thoracic exopodites. The first pair is directed well forwards, taking the place of the reduced and absent exopodites on the seventh and eighth legs, and so project over these endopodites and lie in series with expodites 2 to 6. When swimming the amplitude of the pleopod beat is increased, and the rate of exopodite and pleopod beat may also be increased. The exopodites probably assist the pleopods to some extent in swimming.

Anaspides shows a tendency to progress against the stream under unfavourable conditions, and may crawl out of the water in so doing. Besides swimming mainly with the pleopods, *Anaspides* is capable of extensive and powerful jumping movements in or out of the water when startled. The movement is very rapid, and involves a flexure and tucking-in of the anterior end of the body and a flick of the tail-fan.

The thoracic exopodites and epipodites.—The function of the thoracic exopodites and epipodites appears to be mainly respiratory, and they are probably not concerned in feeding, as was anticipated (Cannon and Manton, 1929, p. 184). The exopodites, as already stated, may be of slight assistance in swimming. The epipodites of the seventh limbs are always stationary, but those of the second to sixth and sometimes the first limbs beat in time with the thoracic exopodites. The epipodites are directed forwards, each proximal overlapping the distal epipodite. They beat inwards and slightly forwards and outwards and slightly downwards. The exopodite beat causes a flow of water along the sides of the body antero-posteriorly only, and does not induce a flow up the axis of the exopodite. Some of this water appears to be caught between the epipodites and the body and passes into the inter-limb gaps. Ventrally these streams flow away from the body into the surrounding water; they are feeble, but remove any water containing a fine suspension from the inter-limb gaps. The absence of a stream passing forwards along the "ventral groove" is equally clear. The limb bases of the anterior segments are usually closed apposed, leaving practically no space between them, and there is no anterior suction along the "ventral groove" caused by the maxilla (see below, p. 796). Thus water-currents around the exopodites and epipodites are not concerned with feeding.

The circulation of the blood probably indicates the main function of the epipodites. The general circulation of the blood resembles that of a Mysid without the carapace circulation. Blood flows from behind forwards in the mid-dorsal part of the abdomen and supplies the pericardium posteriorly. Laterally the pericardium receives streams of blood up the sides of the second to eighth segments. Similar streams flow up the sides of the posterior parts of the abdominal segments and pass into the dorsal space. Ventrally there is a forward stream along the abdomen above the nerve-cord. On reaching the thorax part of this stream is carried sideways to the bases of the limbs, and on reaching the epipodites the blood flows round their margins and then continues up the lateral channels to the pericardium. In the proximal epipodite the blood streams first along its lower margin and back by the upper margin, while in the distal epipodite the blood passes first along the upper margin. Some blood passes across the epipodites through fine channels which

permeate the appendages exactly as does the network of vessels in the respiratory carapace of a Mysid. The rate of flow of blood in the heart, in the pericardium, up the sides of the thorax, and round the epipodites is rapid. It is much slower in other parts. The ventral abdominal flow is slow, but on reaching the thorax, where it divides to supply the limb-bases, it suddenly quickens. In all limbs the flow is slower than in the epipodites—a corpuscle circulates round an epipodite in 1 second or less, while it takes 5–6 seconds to pass halfway down a pleopod and back. The rapidity of flow through the epipodites may be due to the suction exerted by the pericardium, but it is also aided by the beating of the epipodites themselves. When the epipodites are still and the heart normal, the flow round the epipodites is slower than when the epipodites vibrate. However, in the small seventh thoracic epipodite, which is always stationary, the circulation is always rapid. The cuticle of the body, with the exception of the epipodites, is very thick, and the epipodites are the only places where the blood comes in close contact with the surrounding water. The very efficient blood circulation through these appendages and the efficient change of water around them suggest that the epipodites have a respiratory function. In both these features the epipodites resemble the respiratory carapace of a Mysid.

Feeding habits.—*Anaspides*, although possessing a maxillary filtering mechanism, does not filter the water in which it swims as does *Paranaspides*, a Mysid, or a Euphausid; but the maxilla, with its filter-plate and valve, plays an important part in the feeding off "large" food. Facts demonstrating the absence of a filter feeding habit, although the mechanism is present, were these:—(1) The streams caught by the epipodites do not unite to form a food-stream and are feeble; and there is no rotatory action of the exopodites (see above, p. 795), although the presence of forwardly projecting epipodites might render this unnecessary for obtaining currents entering between the legs. (2) The mouth-parts are not used when the animal swims or walks and is not manipulating food-masses, and the bases of the first pair of thoracic limbs are held close together. Thus there is no anterior suction along the ventral groove between the limbs caused by the maxilla as in a Mysid, and water is not filtered by the maxilla during swimming, as the mouth-parts are stationary. (3) Animals were kept in suspensions of iron saccharate under various conditions, and showed no trace of iron being taken into the gut or clogging the setæ of the mouth-parts even after the animals had been living healthily in the suspension for two days. A filtratory crustacean may fill its gut completely with iron saccharate within half an hour of being placed in the suspension.

Anaspides normally feeds upon algæ and detritus covering weeds and stones over which the animal walks, and when adult upon small organisms such as tadpoles and worms. The gut-contents showed tufts of minute branching filamentous algæ, one cell thick, smaller pieces of more substantial algæ, bits of plant tissue, and much unrecognizable detritus. On Mount Wellington the abundance of tadpoles in bog-pools was inversely proportional to the numbers of *Anaspides* present. The eyes, although acute, are useless for locating food, as they face upwards and outwards. The tips of the first thoracic endopodites are never used for walking and digging, but vibrate continually with a dabbing movement. They may be sensory. *Anaspides* expends considerable time digging in the mud with the second to fifth thoracic endopodites—scratching in one place, and, if no food is encountered, moving to another. If a tadpole is accidentally trodden on and then lost, *Anaspides* excitedly hunts and scratches for it in the surrounding area regardless of the direction of escape of the tadpole. *Anaspides* is a very clumsy hunter of live prey, as it is apparently unable to see the substratum or to scent food from a distance, and depends entirely on stumbling upon it.

The rectangular mouth-field is bounded laterally by the first thoracic endopodites, anteriorly by the labrum and posteriorly by the endites of the first pair of trunk-

limbs (Cannon and Manton, 1929, text-fig. 3, p. 180). The bases of the first trunk-limbs are held close together, a bulge from the body-wall of this segment closing any space between these limb-bases. This bulge is seen in text-fig. 6, p. 183, Manton and Cannon, 1929, where the limbs are slightly apart, but when feeding no space is left forming an entrance, "*e.n.f.c.*," to the food-chamber posteriorly. When feeding off a flat surface the mouth-field is closely applied to it, the first thoracic endopodites remaining lateral in position (text-fig. 1). Small stones may be picked up by the second to the fifth endopodites while the animal stands upon the sixth to eighth endopodites. The second to fifth endopodites grip the object laterally while the mandibular palps and tips of the first thoracic endopodites manipulate it anteriorly, and various parts are then brought against the mouth-field (Pl. III.). A tadpole or worm is treated in a similar manner, only with more excitement, and the food may be carried away to be consumed in hiding.

Into the mouth-field bite the mouth-parts, details of which have already been given (Cannon and Manton, 1929). The mouth-field is closely applied to the food, which is scraped by the backward and forward movement of the endites of the first trunk-limbs and by a movement in the transverse plane of the spinous bifid tips of the maxillæ. The tips of the maxillæ can be moved in the transverse plane to a considerable extent quite independently of the main endopodite, and the movement of the endites of the first trunk-limb is likewise independent of the endopodite. The food may also be bitten into directly by the incisor processes of the mandibles and disal endites of the maxillules. In scraping up algæ the action of the endites of the first trunk-limbs and of the maxillæ is the most important.

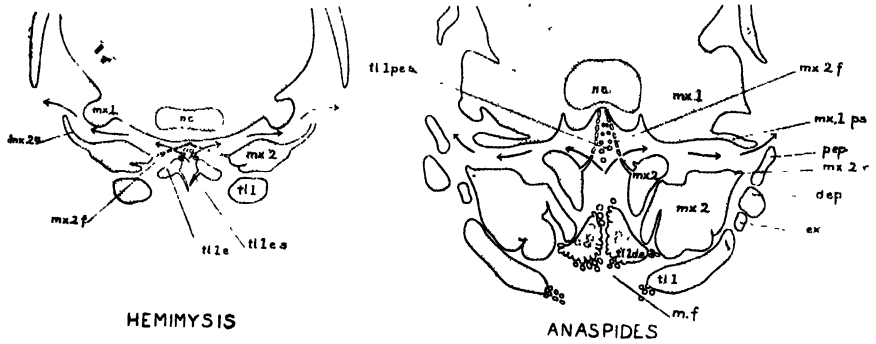
By these actions many small particles of food come to lie freely in the mouth-field, and are unable to escape if the endopodites of the first trunk-limbs are kept in contact with the food-surface or substratum laterally (text-fig. 1, p. 798). It is in the collection of such scraped-up particles that the maxillary filter is of the utmost importance.

Distally the maxilla slopes forwards more than the maxillule, and touches it ventrally. The maxillæ move outwards almost in the transverse plane, and not by an outward and backward motion as in a Mysid. They bite together just before the maxillules meet. The valve formed by the pseudexopodite of the maxillule and the ridge on the outer side of the maxilla is closed when the maxillæ are apart and open when they are together. Owing to the disposition of the parts the space between the maxilla and the maxillule is only open to the surrounding water through the filter-plate on the inner side, and intermittently through the valve formed by these limbs on the outer side. The movement of the maxilla must suck water from the mouth-field region through the filter-plate, as in a Mysid, and so must tend to draw particles in the water down between the filter-plates which are nearly vertical in position. The relative positions of the mouth-parts in region of the maxillary filter-plate can be seen in the text-fig. Food particles are thus concentrated towards the mid-ventral line, where they are transferred to the mouth by the dorsal parts of the first trunk-limb endites and the proximal maxillulary endites. The setose paragnaths are freely movable in the transverse plane, and assist in shifting the food forwards. The labrum is also actively moved. The postero-ventral lip in the middle line is moved antero-ventrally as the mouth-parts are divaricated, and the reverse as they bite together, thus assisting in gripping the food and drawing it into the oral cavity. Thus by maintaining close contact of the mouth field with the substratum, small food particles are first dislodged by the endites of the first trunk-limbs and by the tips of the maxillæ, and then effectively collected by the maxillary filtering mechanism. Without some such effective system small food particles once dislodged would be easily swept away by the fast-flowing water in which the animals often live.

The nearly vertical position of the filter plates makes the collection of food particles by (1) suction, and (2) simple mechanical packing by the approximation of the plates, a far more efficient process than could be obtained by filter plates in the horizontal position seen in a Mysid (text-fig. 1). The maxillary filter plate partly acts simply as a block across the space between the maxilla and maxillule, so preventing particles from entering this space. A similar effect is produced in the Mysid *Lophogaster*, which has no filter plate and is raptatory, by the large swollen proximal endite of the maxillule, which blocks the gap between maxilla and maxillule.

When feeding on algæ covering weed and moss a filament or stem may be passed between the endopodites of the first trunk-limbs, which are then approximated

Text-figure 1.



Transverse sections through the mouth field across the maxillary filter plates of *Hemimysis* and *Anaspides*.

In *Hemimysis* the filter-plates are nearly horizontal, and below them are the paired endites of the first trunk-limbs ("*tl*.1, *e*."), which scrape along these plates.

In *Anaspides* the mouth field is a deep space, bounded ventro-laterally by the endopodites of the first trunk-limbs, which fit closely against the maxillæ. The filter-plates are nearly vertical, and are scraped by the proximal endites of the first trunk limbs ("*tl*.1, *p.e.s.*"), while into the mouth field projects ventrally the distal endites of the first trunk limbs ("*tl*.1, *d e.*").

The outgoing path for the filtered water is comparable in both *Hemimysis* and *Anaspides*, and is indicated by the arrows. An outer valve is formed in *Hemimysis* by the maxillary exite (*mx*.2,*e*.), and in *Anaspides* by the maxillulary pseudexopodite and the outer ridge on the maxilla ("*mx*.1, *ps*." and "*mx*.2,*r*."). Both sections show the valve in its open phase. *c.*, carapace; *d.ep.*, distal epipodite of first trunk-limb; *ex.*, exopodite of first trunk-limb; *m.f.*, mouth-field; *mx*.1, base of maxillule; *mx*.1, *ps*., pseudexopodite of the maxillule; *mx*.2. maxilla; *mx*.2,*e*., maxillary exite; *mx*.2, *f*., setæ forming filter-plate from the proximal endite of the maxilla; *mx*.2,*r*., ridge on outer side of the maxilla; *n.c.*, nerve-cord; *p.ep.*, proximal epipodite of the first trunk-limb; *tl*.1, endopodite of the first trunk-limb; *tl*.1, *d.e.*, distal endite of the first trunk-limb; *tl*.1, *e.*, endite of the first trunk-limb; *tl* 1, *p.e.s.*, setæ from the proximal endite of the first trunk-limb.

and scrape the filament. Usually only the endites of this limb are used for scraping; while endopodite is used to grip and sweep in particles, all its setæ round the mouth-field pointing towards the latter. The first trunk limbs are also frequently used to clean the antennæ, which are drawn between these limbs one at a time.

Colour Varieties.

As has been mentioned above, *Anaspides* appears in two main varieties of colour. A dark brown to olive-green form is found in the dark pools on the top of Mount Wellington (Pls. II. & III.), while in the streams down the sides of the

mountain and in the lower pools the animals are all light brown in colour (Pl. IV.), and the pools here are usually very light in colour also. The *Anaspides* in these light situations, however, are dark enough to be conspicuous against their even lighter background, while on top of the mountain the dark variety closely matches its surroundings. The colour of each animal appears fixed, and small light and dark individuals kept for a short time under different conditions did not appear to alter at all in colour. The chromatophores of the two varieties are very similar in arrangement and distribution, but they are not quite so abundant in the lighter form. The basal colour of the cuticle and tissues of the two forms appears very different, and this is clearly seen in the pleopods, where no chromatophores are present. The dark variety reaches a maximum size of 38 mm. from rostrum to to the tip of the telson, while the lighter variety only reaches a maximum size of 34 mm. No other marked differences could be found between these two varieties, although minute differences in size and number of setæ on some of the appendages are present.

Conclusions.

The habits and movements exhibited by *Paranaspides* and *Anaspides* show several points of considerable interest. *Paranaspides* appears to be a pelagic weed-living animal with filtratory and raptatory types of feeding, either filtering the surrounding water or sweeping up matter from the surface of the weeds. *Anaspides*, although possessing a filtratory mechanism similar to that of *Paranaspides*, only uses this mechanism in conjunction with its raptatory habit. It does not filter the water in which it lives as does a typical filtratory feeder, but only uses the filtratory mechanism to collect particles scraped up by the raptatory parts of its limbs. The raptatory habit of *Anaspides* is more developed than in *Paranaspides*; hence the stronger development of the setæ on the distal endites of the maxillules and maxillæ. The form of the præ-ischial ridge on the first trunk-limb, and the position of the latter, is also correlated with the raptatory habit—in *Paranaspides* for sweeping narrow stems, and in *Anaspides* for keeping the mouth-field ventro-laterally in close contact with the substratum, and also for sweeping.

The independent action of the maxillary filtratory mechanism in *Paranaspides* and in *Anaspides* is of interest, since, as already suggested (Cannon and Manton, 1927, p. 237), such a condition probably preceded the *Hemimysis* type, where the maxillary filtratory mechanism is aided by an auxiliary thoracic food-stream created by the thoracic expodites. The primitive Mysid *Gnathophausia* is the only other Malacostracan investigated in which the filtering mechanism is independent (Manton, 1928, p. 108). The independence of the maxillary filter in *Anaspides* and *Paranaspides* is correlated with the very simple type of beat shown by the thoracic expodites. It is reasonable to suppose that such a simple antero-posterior swing of the expodite may have been shown by the early Malacostraca, and also perhaps may exist in the living *Gnathophausia*. Only a slight alteration of this movement would lead to a rotatory beat in an elliptic path—this is even shown occasionally by *Anaspides*. Once a rotatory type of beat was established, as in most filtratory Mysids and Euphausids, then the possibility would arise for the utilisation of these limbs to create an auxiliary thoracic food-stream. Water would pass up the cone of rotation of the limb into the inter-limb spaces, and then be directed forwards along the "ventral groove" by some other contrivance, such as the position and shape of the limb bases or the positions of the inter-limb spaces.

The utilization of the thorax and abdomen in *Anaspides* as a single functional region in walking and swimming is noteworthy. This is quite unusual in living Malacostraca, where the two tagmata are distinct both morphologically and in function. This peculiarity may be due to the persistence of functional continuity exhibited by early Malacostraca before the morphological distinction

between the two tagmata became very marked. On the other hand, it is possibly correlated with the predominant crawling habit of *Anaspides*, which may have been derived from a swimming life such as shown by *Paranaspides*.

The persistence of crustacea as unspecialized in habits as *Anaspides* and *Paranaspides* at the present day is associated with their peculiar habitat. *Paranaspides* is apparently well protected by the weeds, and there are few large predatory fish in the Great Lake apart from the recently introduced brown and rainbow trout. *Anaspides* has apparently lived on Tasmanian mountains undergoing little change since Carboniferous times. Its survival may be correlated partly with the absence of competition in these pools and streams. It has no predatory enemies, and the pools contain only a few amphipods and worms apart from microscopic fauna. *Anaspides* is indeed quite incapable of meeting competition—a caddis-larva one-quarter the size of *Anaspides* can kill the latter instantly and without protest, and attention has already been called to the inefficient method displayed by *Anaspides* in hunting for large food.

Literature List.

1927. Cannon, H. G., and Manton, S. M. On the Feeding Mechanism of the Mysid Crustacean, *Hemimysis lamornæ*. Trans. Roy. Soc. Edin. vol. lv. pp. 219–254, pls. i.–iv.; 16 text-figs.

1929. Cannon, H. G., and Manton, S. M. On the Feeding Mechanism of the Syncarid Crustacea. Trans. Roy. Soc. Edin. vol. lvi. pp. 175–189; 8 text-figs.

1928. Manton, S. M. On some Points in the Anatomy and Habits of the Lophogastrid Crustacea. Trans. Roy. Soc. Edin. vol. lvi. pp. 103–119, pls. i.–iii.; 2 text-figs.

1908. Smith, G. W. Preliminary Account of the Habits and Structure of the Anaspididæ, with Remarks on some other Freshwater Crustacea from Tasmania. Proc. Roy. Soc. London, ser. B, vol. lxxx. pp. 465–473, pl. xiii.

1909. Smith, G. W. A Naturalist in Tasmania, pp. 1–151, figs. 1–35. Oxford.

EXPLANATION OF THE PLATES.

Plate I.

Immature and adult *Paranaspides lacustris* from the Great Lake of Tasmania.

Plate II.

Dorsal view of the dark variety of *Anaspides tasmaniæ* from the top of Mount Wellington in its resting position.

Plate III.

Lateral view of the dark variety of *Anaspides tasmaniæ* at rest feeding upon a tadpole.

Plate IV.

Light variety of *Anaspides tasmaniæ* from the slopes of Mount Wellington below about 2000 ft.

37. Animal Life in the Marsh Ditches of the Thames Estuary.

By F. J. LAMBERT *.

(With one Map.)

[Received March 11, 1930: Read April 15, 930.]

CONTENTS.

	Page
I. Introduction	801
II. Topography of the Area investigated	801
III. The Origin and Evolution of the Marsh Ditches	803
IV. Animal Life in the Marsh Ditches	804
V. Notes on the Leigh Ditches	806
VI. Summary	808

I. INTRODUCTION.

The main object of this paper is to give a description of the animal life in the marsh ditches of the Thames Estuary, and of the adverse circumstances in which many members of the fauna find themselves. Where necessary, notes on the plants of this area are introduced in order to make as complete an ecological picture as possible. The data here supplied have been obtained as the result of personal observation and experience covering a period of 10 years (1920–1929).

The peculiar, and in many ways, highly exacting conditions of life found in estuaries have been already noticed in works of ecology and distribution (*cf.* Robson, "The Animal Life of Estuaries," Journ. Quekett Micr. Club, (2) xv. p. 161, 1925). Owing to the circumstances in which the author has been compelled to work he has had little opportunity of studying the literature on marsh faunas in other areas. He is, therefore, not aware to what extent fluctuations in environmental conditions similar to those described in this paper may have been observed elsewhere; but it seems that the exceptional local conditions and the special history of the formation of the Thames marshes are sufficiently interesting for publication without discussion on their general ecological importance.

The thanks of the writer are due to Dr. Calman, F.R.S., and Messrs. Gepp and Monro, of the British Museum (Natural History), for their kind identification of animals and plants from the ditches, also to Mr. Percy Thompson and Miss Greaves, of the Essex Museum, Stratford, for similar assistance and advice.

Especial thanks are due to Mr. Robson, of the British Museum (Natural History), not only for the identification of material submitted to him, but for his advice, kindly criticism, and personal assistance in the preparation of the paper, which, indeed, without his encouragement would probably never have been written.

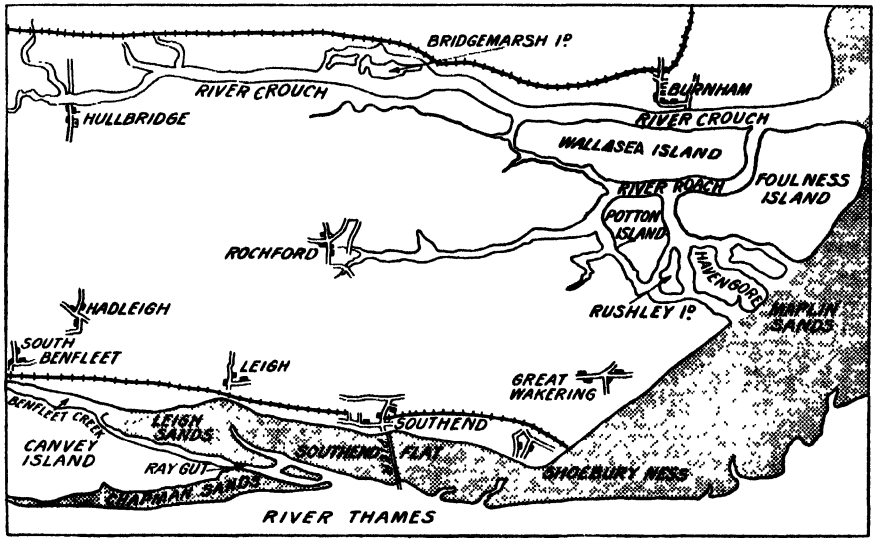
II. TOPOGRAPHY OF THE AREA INVESTIGATED.

The area which is discussed in this paper includes the S.E. coast of Essex from Foulness Island on the east to Benfleet on the west. It does not include Canvey Island. In this area two stretches of marsh are found. The first, seen between Foulness and Shoebury (about 12 miles), apparently originated from the conjoined

* Communicated by G. C. ROBSON, M.A., F.Z.S.

deltas of the Roach, Crouch, and Thames rivers. At present this area consists of numerous islands all protected by dykes and separated by passages or creeks linking up the rivers named. Of the creeks, Havengore is now the only one open which gives access to the Thames. The others, Shelford Creek and New England Creek, have been dammed by order of the War Office. The former is a paradise for those interested in marine faunas in a transitional stage.

The mainland part of this marsh extends from Wakering to Wallasey. The mainland itself lies to the west of these islands and marshes, the north side of the marsh-area being bounded by the River Crouch. It is uncertain what land movements are taking place, but north of the Crouch, in the Dengie hundred, it is thought that subsidence is in progress. Certainly the sites of the villas of the Roman city of Oithona are only visible at low tides. Westwards from Shoebury, the soil of which is sand and shingle with a foreshore of arenaceous mud, the land



Marsh areas, Leigh to Benfleet and Wakering to Foulness *.

rises into fairly high uplands (London clay, sometimes topped at places with gravels and sands) faced with reclaimed and unclaimed marsh. Farther to the west at Southchurch and Southend the marsh has been built over and modified by urban development.

Beyond Southend one enters the second area of marsh at the foot of the higher uplands from Leigh to Pitsea (and indeed to Mucking), a very large area. For the purposes of this paper the area is limited by a line drawn north through Benfleet.

At Leigh the railway to London cuts across the marsh. The raised permanent way with its projecting banks, separates the ditches which meander through the marsh into brackish ditches on its south side and freshwater ditches on the north side.

* New England Island lies between Havengore Island and Foulness Island. Shelford Creek separates it from Foulness Island and New England Creek (now enclosed) isolates it from Havengore Island. A concrete road now links up all three islands with the mainland. *Priapralus* can be found in Shelford Creek.

III. The Origin and Evolution of the Marsh Ditches.

The origin of most of the marshes of the Thames Estuary is the same. In the course of a long period of time, varying in duration according to the volume of flood-waters and the openness to the sea, the littoral becomes banked with mud* traversed with swins, gullies, and runnels, and rises little by little. *Zostera* gives way to *Enteromorpha*, and *Enteromorpha* to the plants of the low marsh, particularly to *Obione*, *Salicornia*, the Sea Aster, Sea Lavender, and the grasses (*Spartina* etc.) of the saltings. These plants hold the silt which becomes consolidated into mud and bound with roots which eventually become peat. As the vegetation holds, the gullies, with the drainage of the marsh, cut deeper until what was once the level bed of a wide shore, or of a deep stream, becomes a series of islands daily growing higher out of the water and separated (except at low tide) by miniature lakes and rivers. When the expanse of marsh is sufficiently large to cause covetous eyes to be cast upon it, it is taken in hand and a wall of its own soil raised round it higher than the water at high spring tides and set well back from its outer edge. On each side of the wall is a broad and sometimes deep ditch, the bed of which is always very soft, being formed of the underlying clay which has never dried, and into it on the inside run the old swins, gullies, and runnels which used to run to the sea and now only take off the rain-water from the land.

For some years after the reclamation but little change takes place owing to the sodden condition of the ground†. On the drier parts the Sea Lavender, *Obione*, and the marsh grasses flourish. In the old gullies (now ditches), *Salicornia* and Sea Aster with *Ulva* and *Enteromorpha* still survive, together with crabs, prawns, gobies, *Nereis*, *Littorina*, *Paludestrina*, *Alderia*, and *Limapontia*, and other marine forms, trapped during the process of "inning."

But changes are at hand. As the land dries, sheep and cattle are sent out. The Sea Lavender is devoured and *Obione*, dwarfed by drought, is either eaten or stamped out. The ditches become sterilized by alternate floods from rains and salt water from the sluices in the sea wall; the old flora and fauna die out and are replaced by seasonal ones able to exist just for as long as their appropriate conditions persist in the ditches.

Wading birds like the Heron introduce new seeds and eggs, the wind-borne flora now finds a congenial soil, the reed appears and eventually fills the ditches, and the sloe (more often than not sterile) borders them. The grass grows out into them, and the bottoms rise with decaying vegetation until, after the passing of years, the shallower runnels are filled up and are only made visible by the drainage water covering the outline of their old course in the winters‡.

And this is not all. The marsh becomes the farm; the land is put under the plough and sown with grass and corn, and, because the land must be well drained, straight ditches are cut at right angles to the main ditch by the dyke wall. So "the marsh" finally passes, though the sea sometimes recovers its domain, as at New England, at Maldon, and at Canvey. Also important changes take place in the relation of levels between the new land inside the wall and the old marsh outside.

Inside the walls the land is cropped incessantly, and so its level never rises, but rather tends to sink by dryness and compression of the peat underneath. Outside, the river and its tides daily bring to the river-bed and its marshes their load of silt; and so with time both the bed and the low marsh tend to rise, and eventually the bed of the river is in height many feet above the level of the

* In most estuaries the tide ebbs inshore first, sometimes three-quarters of an hour before it does in the river fairway; this causes an eddy which deposits silts.

† As at Creeksea, Wallasey Island (Essex), also the banks of Benfleet Creek, outside the wall.

‡ Leigh and Hadleigh marshes would appear from old engravings dated 1832 to be nearly 100 years old, but the old creek leading to Hadleigh Castle becomes visible once again after heavy rains in the winter.

reclaimed land, as at Leigh, Havengore, and New England, and the water from the sluices draining the land has to pass away through channels many feet deep in the more recent alluvium outside. These sluices are generally iron pipes capped and hinged at the end so that at a sufficient depth, if working properly, pressure closes the cap and prevents ingress of the river or sea to the land, whilst not obstructing the drainage water escaping at low tide, and it is through these channels and pipes that most of the marine animals in the ditches have to come.

IV. Animal Life in the Ditches.

It will be obvious that an important part will be played in the animal life of the ditches by the varying salinity of their waters *. This will be determined by the salinity of the tidal waters outside and the extent to which they have access to the ditches, by rainfall on the land, the strength of the wind, the amount of sunshine causing evaporation, and the time of the year, for all the water has to pass through the ditches, and, with a series of high tides and the high river-bed, it may not be able to escape easily; whilst at the same time the same winds which cause the pent up waters may bring heavy rains which flood the land. With changes of such violence it is theoretically probable that a fauna able to endure them must be few in species and sometimes sparse in members. This is actually what I have found.

Conversely, at times when the external pressure on dykes riven by contraction-fissures causes the walls to give way and the sea breaks in, ponds and ditches of normally fresh water are for a longer or shorter period markedly saline. Nevertheless, the water draining into such ponds and ditches from the land sooner or later reasserts itself, and the salt water is gradually diluted, and but few marine animals, so far as I have seen, succeed in maintaining themselves in their new habitat of *pure sweet* water. The animals which do so are *Palæmonetes varians*, *Neomysis*, the 3-spine Stickleback, and the Eel. I know of no others, but it is possible that other forms do survive in some of the ponds and ditches.

A single example will illustrate the association and habitat under discussion. At Kearsey's Marsh, Benfleet, on the land side of the railway and towards Leigh, is a square pond connected with a ditch, once part of a brickfield. It contains pure water † drunk by horses and cattle. Here occur three of the forms just mentioned, survivors of inundations in 1902 and 1907 from the Ray. The chief water-plant is *Potamogeton pectinatus*. *Enteromorpha* greatly changed is also present. *Palæmonetes varians* is there in thousands, half a mile from the sea-water. It is glass-like in appearance and only visible from above by the black mud in the stomachs (apparently the only food). They breed abundantly. *Neomysis* is not so plentiful. No other inhabitants were observed. Eels, however, were known to be present.

A factor which I think influences the flora, and through the flora the fauna, is the nature of the mud at the bottom of the ditches. Having once been tidal banks, all the marshes will contain shells of various species and, therefore, lime. The soil of Canvey Island is full of cockle shells. At Leigh few cockles are found, but *Mya*, *Scrobicularia*, and *Tellina* occur, all having hard shells which resist decomposition. At New England and Havengore, oysters and *Crepidula* seem to be present in good numbers and in a very decayed condition. Besides this there is decayed débris from the vegetation, and, in some soils such as that of the Leigh ditches and Shelford creek, very much iron, which is probably being fixed by the action of bacteria. This is most pronounced where the bed is very soft from the presence of silt and the decay of the local vegetation. It seems largely absent in ditches periodically cleansed (by digging) by the farmer at Leigh and by the War Department along the roadside towards Havengore Bridge, at Wakering, where

* The variation is very great in the Thames Estuary, viz. 1·028 in a normally dry season to as low as 1·010 off the "Mouse" lightship on one occasion.

† See note in 'Essex Naturalist,' xix. pt. v. p. 328.

the ditch-beds appear greenish yellow in colour, as against the reddish brown of those untouched.

That the pollution of the soil affects the flora would seem proved by the fact that I have failed to get *Chætomorpha linum*, which exists in masses in Wakering ditches, to establish itself in the Leigh Marsh ditches, the Wakering ditches being "clean," the Leigh ones polluted; but it is possible, however, that evaporation in the Wakering ditches, which are well inland, and the clear water produce the conditions essential to life, as *Chætomorpha* likes, and can endure, very high salinity, bright light, and heat *.

The condition of the mud must also affect to some extent the mollusca and worms which live in it. I have seen the shells of *Paludestrina ulvæ* quite red with rust †. As a matter of fact, the predominant colour of the shells of these molluscs is reddish. At various places in the Leigh ditches I have seen both the bottom and the vegetation very rusty, and in Shelford Creek, Foulness side, there were patches where rust was actually oozing away at the surface, though, delving with a trowel under the patches, I failed to disclose any spring or anything other than ordinary surface drainage. On the Leigh open mud-flats old tube-casts of worms where the soil is denuded after storms stand out of the surface as iron sand, and iron pyrites is quite common in the form of nodules and finger-like shapes.

In these enclosed ditches in hot weather an incessant struggle exists for oxygen. The weed, especially *Vaucheria*, the nether masses of which are almost always buried in putrid mud, grows luxuriantly in the hot sunshine and rapidly evaporating water, which, brackish at first, becomes very salt at last. The plant in masses turns reddish, then pale yellow, and dies, poisoning most of the life which it had previously helped to preserve. At Wakering I have seen large eels lying with more than half their bodies out of water which was red (? with algæ or rust) and *stinking*. When pushed back into the water they crawled out again. At Leigh, in the artificial ditches I have seen *Gasterosteus* lying dead in hundreds from the same cause, yet in the putrid mud hundreds of *Paludestrina ventrosa* were still alive and apparently unharmed. Crustacea are not noticed on such occasions; either they withdraw in time, or their bodies are not noticeable ‡.

It will be noticed that the observations recorded above refer to the putrefaction of vegetation; yet also great loss of life takes place through high salinity and desiccation. The Mollusca generally do not appear able to sustain high salinities. I have seen in the middle of Havengore Island a large colony of *Cardium edule* dead (1921) through high salinity, the water not otherwise being bad, and I have also seen in the ditches, recently cleaned, large masses of *Chætomorpha linum* in a rapidly reducing quantity of crystal-clear water of the high salinity with numbers of *Gasterosteus* (3-spined) striving to find a way out of the water in vain.

In one case at least it is interesting to note that an aquatic animal exposed to the danger involved in the periodic drying-up of its habitat apparently survives in great numbers because it has acquired amphibious habits. This form is *Paludestrina ulvæ*, which, in my experience, has a definite objection to continuous immersion in water.

I think that wherever this mollusc occurs it will be discovered to spend at least 20 hours of the 24 in direct contact with air, even if it must be moist air. If it is in tidal water it will be found thus long, uncovered. If in stagnant water it will crawl out and sometimes remains out so long as to die. *Littorina rudis* perishes in the same fashion occasionally. In artificial conditions it crawls

* Perhaps the absence of iron from the cleansed ditches is also a factor.

† *Vaucheria* in my jars apparently caused a heavy deposit of rust to collect on the glass wherever a piece of limestone touched it; and mud from Shelford creek leaves a line of rust on the glass of the jar containing it at the line of the surface of the mud.

‡ I have, on the other hand, found numbers of *Stratiomys* larvæ at Wakering living amid putrescent vegetation, and *Corophium* lives under similar conditions at Leigh.

out and attaches itself by a film. In nature it would probably be recalled to activity by rain, which would moisten the film and cause the mollusc to drop on damp ground and so recuperate *.

In a normal way rain is received in these ditches so gradually as not to cause great harm. As a matter of fact, it does not appear to be obnoxious to many creatures to which tap water would be fatal †. Starfishes on sandbanks and mudbanks and *Actinia mesembryanthemum* on rock, Nereids in mud, besides Fucoids, *Enteromorpha*, and other plants, must often be literally deluged with it—yet they survive.

It is doubtful whether non-saline water ever reaches the ditches in sufficient masses to be fatal to the fauna. The creatures disliking a low salinity usually have time to retire to the sea-wall, where, it is conceivable, they may be washed out to sea through the sluices. A case of very great biological interest in this connection exists in the dammed portion of New England creek, Essex. Originally a free passage from the Thames to the Crouch *via* the Roach, and receiving water and animal life from both directions, it has been dammed at each end of the island by order of the War Office. The western end was designed for a sluice, which, when made, could not be used for fear of washing away the "footings." It has, therefore, been definitely sealed, and the creek, full of truly marine creatures, is now a lake taking the drainage (not purely fresh, owing to the island having been "drowned" for so long, since 1897) of the island. It contains Flounders and other flatfish (some known to be still alive), Oysters, *Sabella*, Tunicates, Nereids, *Crepidula*, *Amphitrite*, Whelks, Crabs, and probably many other forms, including bivalves. The water is very brackish. It would be very interesting to know if this fauna is still alive, but a proper dredge would be necessary, with a boat (at present there) and War Office permission.

At Hadleigh Marsh many of the cross ditches on the south side and all on the north side of the railway are now fresh water, with a purely freshwater fauna, except in the case mentioned at Benfleet (Kearsey Marsh). Water Grasses abound with Rushes, Water *Ranunculus*, *Callitriche*, Mosses, *Lemna*, *Potamogeton*, *Juncus* and *Arundo*, but no *Anacharis*, though I attempted its introduction out of curiosity. Of animals, I have found *Dytiscus*, *Gasterosteus* (3-spined and 10-spined), Dragonfly larvæ, Caddis, Mayfly larvæ, Bloodworms (*Tubifex*), Eels, etc.—a true freshwater fauna and flora.

As will be seen, the life in the brackish ditches will be largely seasonal, and, as regards the marine forms, somewhat dependent on the time when certain species come close into the coasts. The main ditch, never becoming dry and caked, but receiving each tide at least a modicum of new water, becomes a factor in the distribution of the species.

V. Notes on the Leigh Ditches.

In Mr. G. C. Robson's paper on the succession of *Paludestrina ulvæ* and *ventrosa* (Ann. & Mag. Nat. Hist. 1920) appear lists of the fauna and flora of the Leigh ditches. As he states, they are not complete. The forms recorded in my notes for these ditches may be added to Robson's lists:—

(1) 2/4/1922. Examined main ditch, Leigh Marsh; found a few Gobies only, no Prawns or Sticklebacks; found specimens of *Alderia modesta* and *Limapontia nigra* (first time for 2 years).

(2) 29/4/22. Main (Dyke) ditch; *Palæmonetes varians*, *Gobius minutus*, *Spheroma rugicorda*.

* In South Africa (Durban) a mollusc, probably *Cerithidea*, climbs out of the mud and up the stems of the mangroves, remaining suspended in thousands from the undersides of the branches until they eventually drop off dead.

† Fresh water is stated to kill Starfish instantly, and anemones are likewise destroyed by it to my knowledge.

(3) 28/5/22. Main ditch; *Palæmon squilla*, small 3-spined Sticklebacks, also a few of breeding size, *S. rugicorda* and a few *serratus* (rarer), 1 Eel (3 inches), no Gobies, no *Corophium*, millions of *Paludestrina*—in proportion, 150 *ulvæ* to 15 *ventrosa*.

(4) 3/3/23. Searched Leigh main ditch for *Corophium*; found none; *G. minutus* and a few largish Sticklebacks found. Afterwards went to side ditch (west) for larvæ of Chameleon-fly, but found none. Brought up mud containing *Alderia modesta* and two *S. rugicorda*.

(5) 24/3/23. Visited main ditch, Leigh; found *G. minutus*, Stickleback, *S. rugicorda*, and *Idotea*, but no *Corophium*; noted bed of ditch black and rotten, with patches of grey fungus.

(6) 2/4/23. Visited Leigh main ditch and side ditches; saw no *Corophium*; found large Sticklebacks, Gobies, *Idotea*, *P. varians* in numbers in side ditches, with beetles and four larvæ like Leather Jackets, but not apparently the larvæ of Dronefly (Rat-tail larvæ).

(7) 4/3/23. Rode to Wakering and examined ditches. *Vaucheria* in plenty, animal life scarce: *P. varians*, a few Sticklebacks, *P. ventrosa* in abundance, mostly floating. Obtained a water-boatman (*Notonecta*) and *Hydrophilus*; saw no *Stratiomys* larvæ nor pupæ; nothing but *P. ventrosa* on weed pulled up.

(8) 13/1/29. Visited main ditch Leigh, high tide, but very little water coming through sluice. Surface of ditch covered with thin film of ice; no trace of animals save worms and *Scrobicularia* from their tubes; shrunken and crinkled *Ulva* the only weed. Ditch filled with refuse.

Thus it will be seen the inhabitants generally of the marine ditches are as follows:—

Pisces.....	*Gasterosteus* (3-spined), *Gobius minutus*, and Eel.
Molluscs .	*Scrobicularia*, *Cardium*, *P. ulvæ* and *ventrosa*, *Littorina rudis* var. *tenebrosa* (Wakering), *A. modesta*, and *Limapontia nigra*.
Vermes ...	*Nereis diversicolor* and *pelagica*, Nematoda
Crustacea.	*Carcinus mœnas*, *Idotea*, *Gammarus*, *Spheroma*, *Corophium*, *Palæmonetes varians*, *P. squilla*.
Insects ...	*Hydrophilus*, *Stratiomys*, Dipterous flies, *Notonecta*.
Plants ...	*Ulva lactuca*, host to *Paludestrina ulvæ*, *Vaucheria marina*, host to *P. ventrosa*, *Chætomorpha linum*, host to *Littorina rudis* var. *tenebrosa*, *Enteromorpha*, host to *Alderia modesta*, *Limapontia nigra* (and at Shelford Creek to *P. ulvæ*). *Ruppia maritima* (to which a Dipterous fly larva attaches itself). *Schlerochroa maritima*.

The *Corophium* mentioned are exceedingly interesting, being gargantuan for the species. I have never met with them on flats of the Estuary, which contain the 3-inch vertical burrows of untold myriads of the small variety of *Corophium*. Of the large variety the British Museum possesses one specimen (from Hastings), and Stratford Essex Museum three specimens (from Leigh main ditch). It is quite probable that no more will be obtained from the latter station. To such extent had the inferior antennal legs developed that it was impossible for the creatures to swim normally, and they rolled over and over in progressing. They were visible in one month only of the year (April), when they could be seen swimming and moving along the bottom. They were never abundant. I have never been fully satisfied as to whether they were indigenous to the main ditch or were annual introductions through the sluice, but I am inclined to believe that the former is correct.

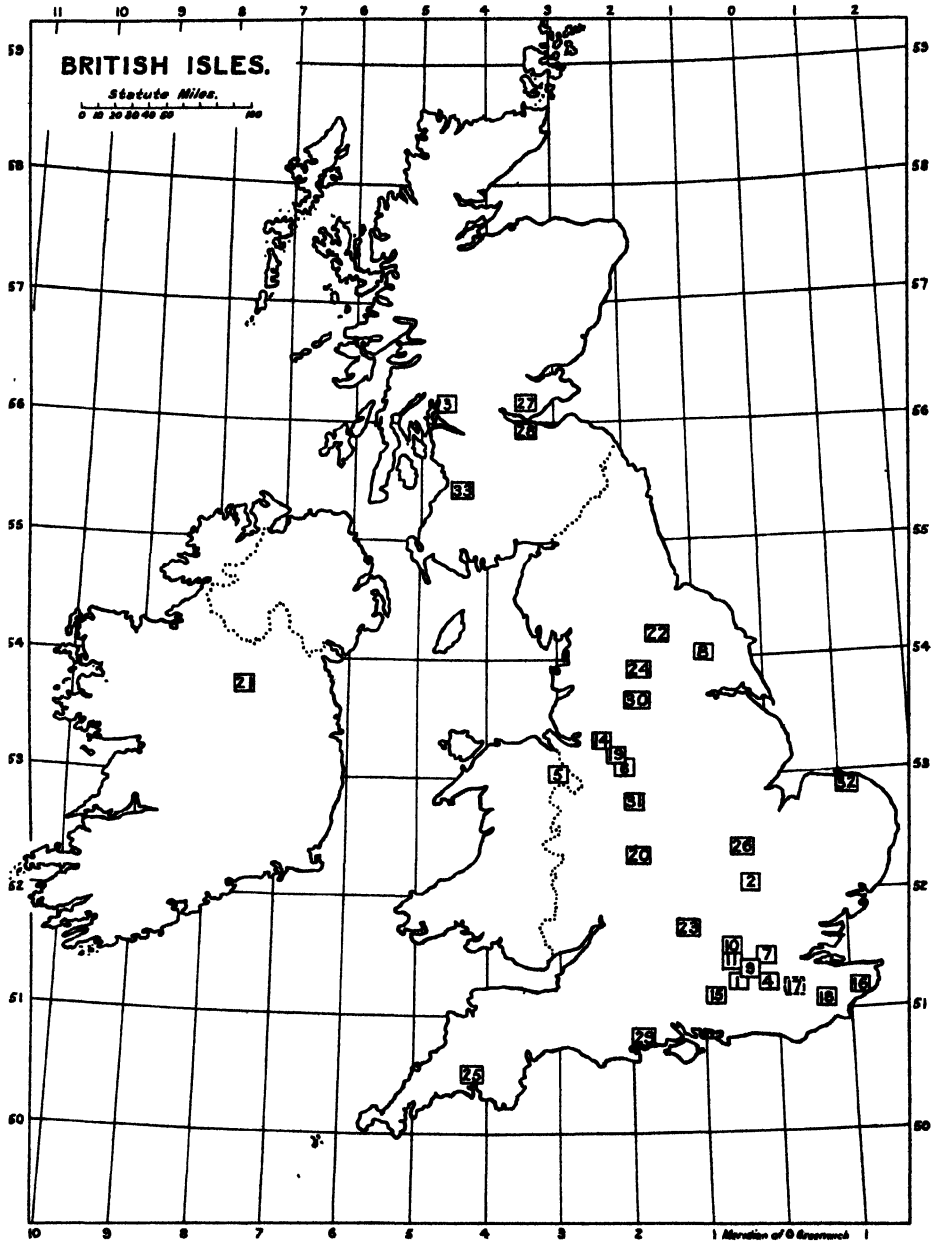
VI. Summary.

1. The formation of the marsh ditches on the Essex side of the Thames estuary is described.

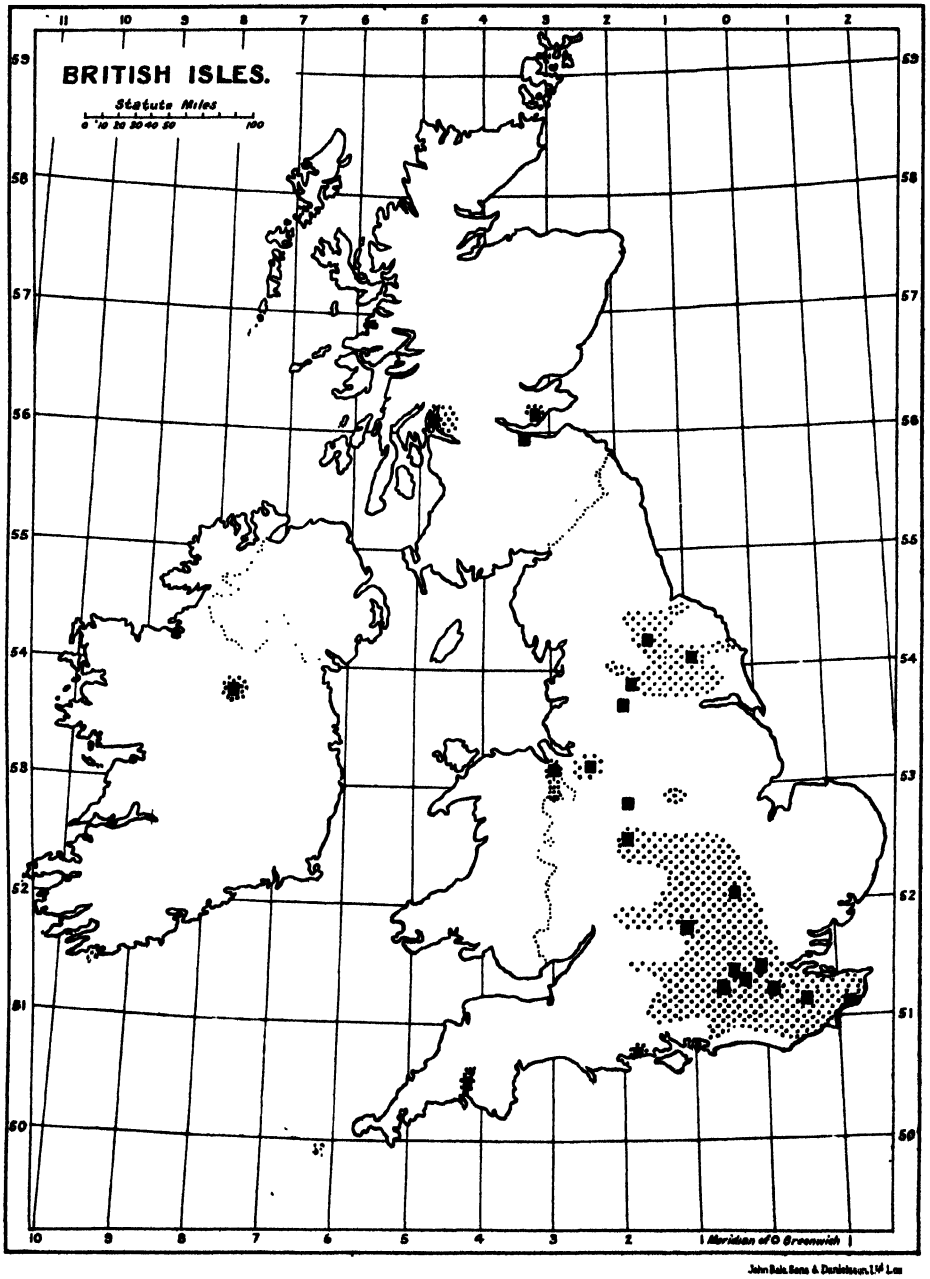
2. An account is given of the progressive reclamation of the marshland and its conversion into arable, and the effect of these processes on the aquatic organisms contained in the drainage ditches of the marsh.

3. The effect of various kinds of organic pollution which occur regularly each year during the hot weather and of periodic changes in salinity are discussed in detail, and the seasonal change in animal life is described.

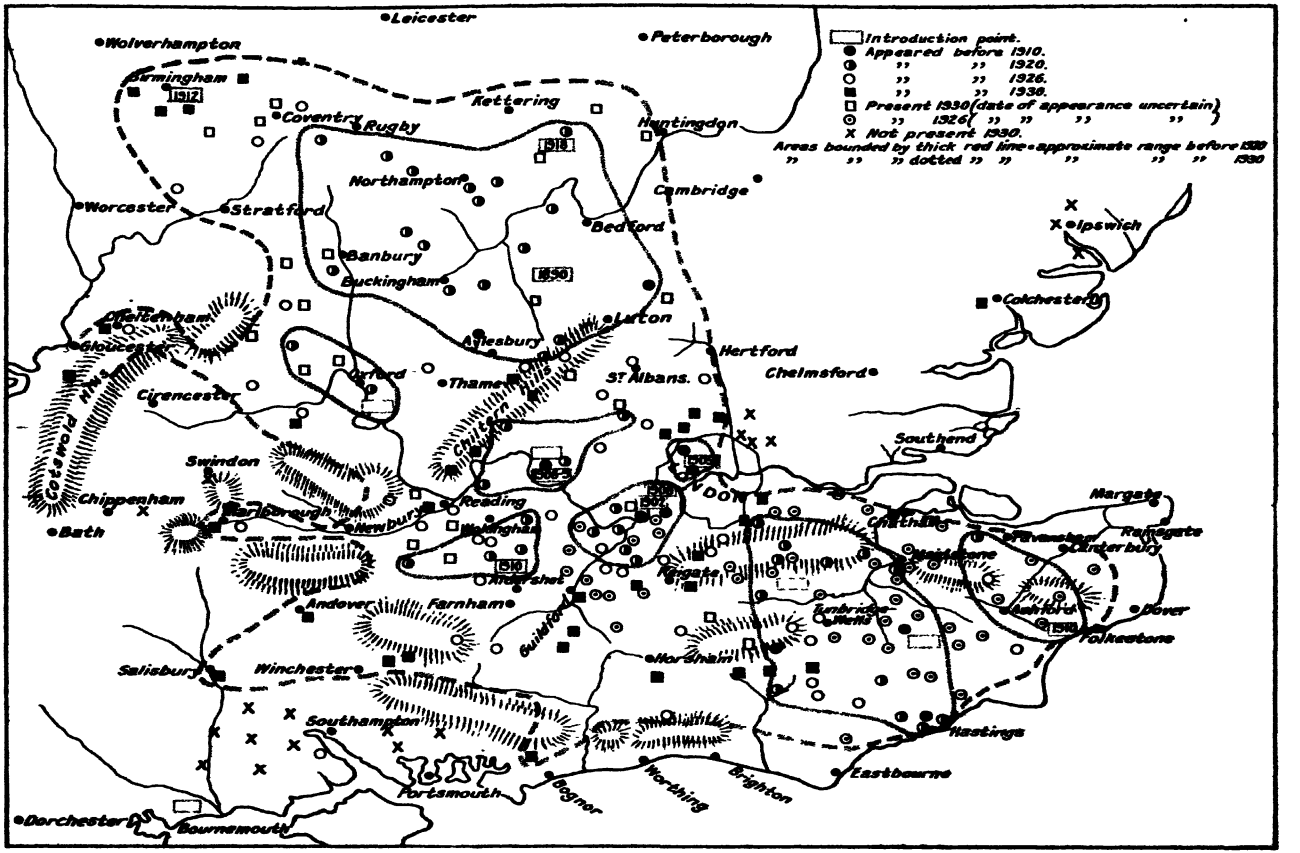
4. Detailed notes on the seasonal changes and faunal succession in the brackish pitches at Leigh are given.



THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.

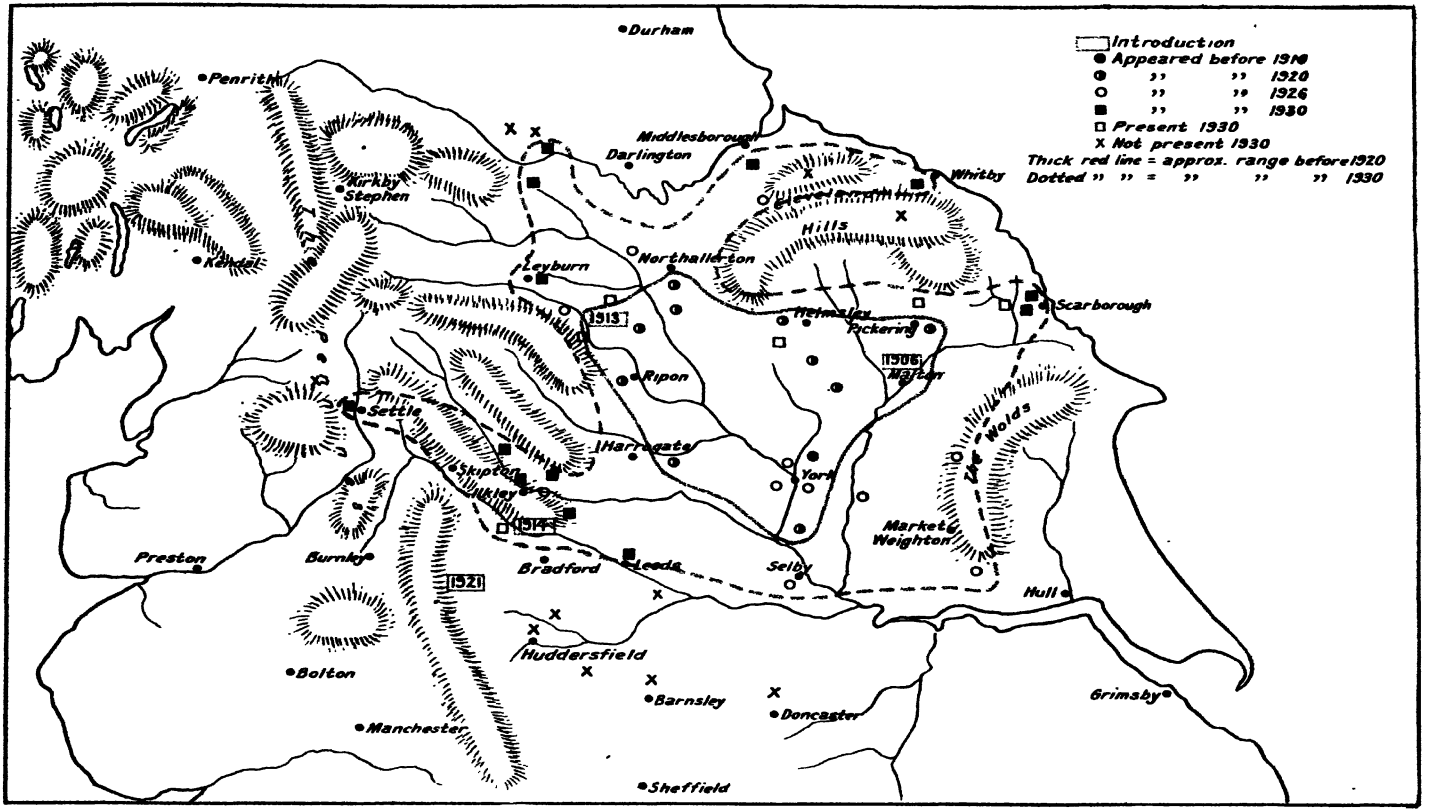


THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.



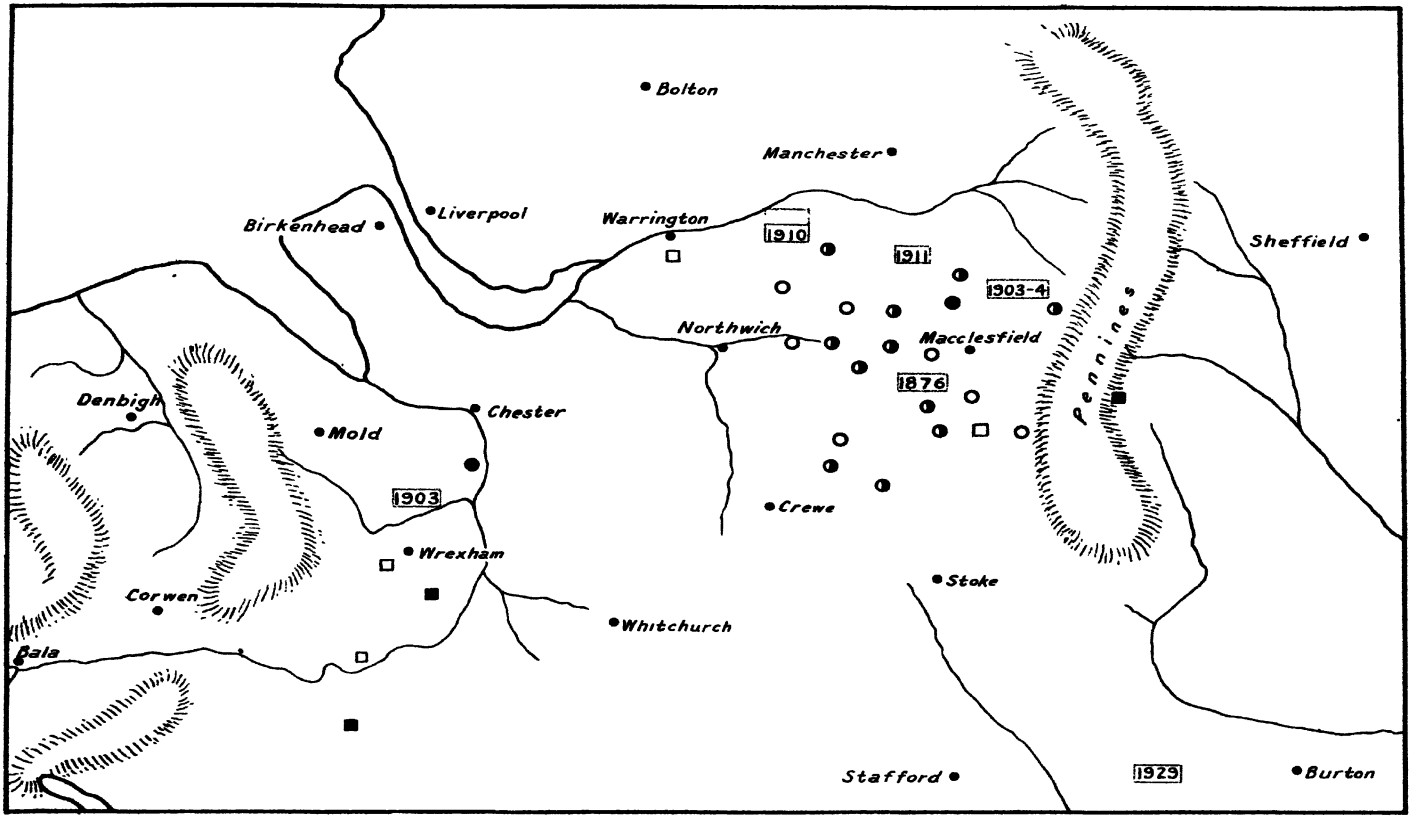
John Bale, Sons & Danielsson, Ltd. London.

THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.



John Bale Sons & Danielsson, Ltd London.

THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.



John Bale Sons & Danielsson, Ltd London.

THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.



John Bale, Sons & Danielsson, Ltd. London.

THE ECOLOGY OF THE AMERICAN GREY SQUIRREL (SCIURUS CAROLINENSIS GMELIN) IN THE BRITISH ISLES.

38. The Ecology of the American Grey Squirrel (*Sciurus carolinensis* Gmelin) in the British Isles.

By A. D. MIDDLETON *.

(From the Department of Zoology and Comparative Anatomy, University Museum, Oxford.)

[Received May 20, 1930: Read May 20, 1930.]

(Plates I.–VI. †; Text-figures 1–4.)

CONTENTS.

	Page
1. Introduction	809
2. Description	810
3. Introduction into the British Isles	810
4. Spread and Distribution	814
5. Habitats	823
6. Habits	823
7. Breeding	825
8. Food and Damage	825
9. Enemies and Parasites	828
10. Seasonal Activity	828
11. Fluctuations and Disease	830
12. Economic Importance and Control Measures	831
13. The Reduction in the Numbers of the Red Squirrel	833
14. Disease among Red Squirrels	833
15. Fluctuations in the Red Squirrel Population	835
16. The Inter-relations of Red and Grey Squirrels	839
17. Summary	840
18. References	840

1. INTRODUCTION.

The investigation which has provided the subject-matter of this paper forms part of a scheme of research into the numbers and fluctuations of wild rodents under the direction of Mr. Charles Elton, to whom my thanks are due for continual advice and assistance. The work is being financed by a grant from the Empire Marketing Board, and has been carried out, by kind permission of Prof. E. S. Goodrich, F.R.S., in the Department of Zoology and Comparative Anatomy at Oxford.

Information regarding the spread of the grey squirrel in the British Isles, and the fluctuations in numbers of the red squirrel and other rodents, has been obtained from a number of correspondents throughout the country by means of questionnaires and through the agency of the Press, as well as by personal interviews and direct observation. My thanks are due to all those who have so readily given me information regarding squirrels in districts of which they have special knowledge; a list is given of the people whose information has been used in compiling this paper, but I must apologise for the omission of the names of many who have given corroborative and negative evidence on certain points, and whose evidence is none the less valuable and appreciated. I wish especially to thank the

* Communicated by THE SECRETARY.

† For explanation of the Plates, see p. 843.

staff of the Forestry Commission for the assistance they have given in this investigation, Mr. R. E. Knowles, the late Prof. Kennedy Orton, Mr. S. Smith, F.Z.S., Major M. Portal, and Mr. F. Faraker for their kindness in undertaking special inquiries in their particular areas on my behalf. My thanks are also due to Mr. Oliver Watney for giving me exceptional facilities and practical assistance in studying the grey squirrels of Wychwood Forest, Oxfordshire.

It is realised that the results of an investigation of this kind can never be said to be complete, and the evidence on such points as the first appearance of grey squirrels in particular districts must always be liable to minor corrections. For this reason negative evidence has, except in certain cases, been avoided in the compilation of maps, tables, etc. Whereas positive evidence of the occurrence of squirrels in a particular district is undeniable, negative evidence is rarely certain and may often be the result of limited observation.

Numerous general reports relative to the food and habits of the grey squirrel, such as "eats birds' eggs" and "has exterminated all the red squirrels," have had to be neglected in this paper, and only the evidence backed by detailed observation is included.

2. Description.

The Grey Squirrel (*Sciurus carolinensis* Gmelin) is a native species of North America, of which there are at least five subspecies with varying distributions. So far as is known, all the American squirrels introduced into the British Isles are *Sciurus carolinensis leucotus* Gapper, which occurs throughout the North-Eastern United States and South-Eastern Canada, Latitude 44°–50° N. and Longitude 65°–96° W. (29).

Adult specimens from Wychwood Forest, Oxon, weigh between 600 and 700 grammes, and the average total length is about 530 millimetres, including the tail length of about 200 millimetres. The general colour effect is silver grey, and white underneath, but in most specimens the head, ears, back, and tops of the feet are strongly tinted with russet-brown, with a line of brown running along the sides next to the white abdominal coat. The individual hairs show three or more colour zones of black, brown, and white, interspersed with a considerable number of pure black hairs. The grey effect is given by the hairs with one or more white zones and white tips, while in the hairs of the russet patches there are no white zones, and the tips are usually brown. The tail hairs of winter specimens from the above locality show six colour zones—beginning from the base: black, brown, black, brown, black, and white tips. The tail hairs average from 40 to 60 millimetres in length. There are no tufts on the ears. Other specimens which have been examined from Yorkshire, North Hampshire, Regent's Park, and South Berkshire also conform to this description.

The russet brown coloration of the head and back of many specimens has probably led to the common belief that the grey squirrel interbreeds with the British Red Squirrel (*Sciurus leucorous* Kerr), as there is no positive evidence that the two species can interbreed. Descriptions of the grey squirrel in its native country show that the brown coloration is identical in the American species also (29). There is probably considerably local and seasonal variation in colour, as among all other rodents.

3. Introduction into the British Isles.

There is little doubt that the present distribution of the American grey squirrel in the British Isles is mainly due to the introductions from 1890 onwards, described below, but there are several records of the occurrence of grey squirrels in this country before that date. The following is an extract from a letter to

the editor of the 'Cambrian Quarterly Magazine' in 1830 (28), for the discovery of which I am indebted to Mr. G. Marshall, F.S.A.:—

"I believe that the grey squirrel, known to naturalists as the *Sciurus cinereus* of Linnæus and *Petit Gris* of M. Buffon, has not been classed an inhabitant of this country, yet in some retired glades of Montgomeryshire and Denbighshire a grey squirrel is found. Between Llanfair Caer Einon and Llan Eurvyl, in the former county, in a line nearly East to West, is a deep woody dingle, called Cwm Llwynog (the Fox's Dingle); its windings are intimately known only to the sportsman, wood-gatherers, and peasantry of the neighbourhood, and the great retirement of the place accounts for the neglect its natural history has experienced; here a grey squirrel lives and breeds. The specimens I have seen were as large as a polecat, or a three-quarters grown rabbit; the head roundish, the eyes very prominent, the ears shorter than the common red squirrel's and not the slightest appearance of tufts upon them; the body and legs of a fine grey colour, the latter short and muscular and furnished with strong claws; there is a beautiful variegation of red along the sides of the ribs, from the elbow to the hind leg; the tail is covered with hair rather longer than in the common sort, and of a mixture of grey and black. The description precisely answers to that of the *Petit Gris*; whether the Welsh animal is one of the same, I venture not an opinion, my object is to call the attention of naturalists to the point.

"Regarding the habits of the grey squirrel, I confess my ignorance, further than that their nests present the same ingenious formation as those of the common species, and upon a natural presumption we may conclude that the grey sort also store up wild fruits against the winter, but whether in the hollows of trees or in magazines in the earth, as is the case with the foreign *Petit Gris*, I have had no means of ascertaining; they are extremely shy on the approach of man, darting through the intricacies of the foliage with amazing swiftness, and taking single bounds of many yards' length. The variableness of our climate considerably influences their season of generation; but the young are usually produced from the latter part of April to the end of May. I have been informed that the grey squirrel monopolizes the woods, and that the common red kind are seldom seen near them, which appears reasonable enough, for the size and strength of the grey animal renders him more than a match for the other.

"I have also seen a very fine stuffed specimen of the Welsh grey squirrel in the possession of a gentleman residing in Chester; it was shot near Llandisilio Hall, Denbighshire, in October 1828."

It is not possible to say with certainty what species these squirrels were, but from the description it seems quite probable that they could have been the American grey squirrel (*Sciurus carolinensis*). No records of its occurrence in that area since this letter was written have been found up to the present (except for the known introduction near Wrexham), but it is by no means improbable that descendants of these gray squirrels may still be present in the "great retirement" of some of the glens in Mid- and North Wales.

In a letter to the editor of 'Country Life' in 1929 (27) Miss P. Francklyn states:—

"My gardener, an old man of 75, born in this part of East Kent (near Canterbury), tells me that there were plenty of grey squirrels "up at Eggarton" when he was a boy. They had always been there. His father and grandfather had seen them, and he was sure they had never come from America. They were about the size of the red squirrel, but he never saw a red squirrel in that part of the country. He had been wood-reeve for many years, and knew the woods and forests intimately. The red squirrels were found in the opposite direction in King's Wood. . . . Eggarton is an extensive tract of forest bearing various names, and so might well be the home of a British grey squirrel. . . . Being firmly convinced that grey squirrels were aliens, I have not studied the local

ones closely to see if there is any difference between them and the descendants of the American variety. I can only say that those I have seen are much smaller than the ones to be found in Hyde Park."

Up to the time of writing I have had no opportunity of examining squirrels from this district, and as no detailed description is available of these ancient grey squirrels it is impossible to express any opinion as to their origin.

In 1884 a pair of grey squirrels were shot at Highfields, near Nottingham, by a correspondent (1) during a visit to that district. Grey squirrels were reported to be present at Bestwood and Hartsholme, near Nottingham, in 1929 (26), and as far as is known form a colony separate from the other centres. Up to the time of writing very little information has been obtained from this district, so that I am unable to say whether the present colony may or may not have descended from grey squirrels introduced before 1884.

At Henbury Park, Cheshire, the history of the grey squirrel goes back to 1876. "Mr. T. U. Brocklehurst brought two back from America, kept them in a large cage on the wall of the house, and exhibited them to his friends until, tiring of them, they were liberated into the adjacent woods (in 1876). Mr. T. U. Brocklehurst died in 1886, being succeeded by his son, Mr. W. W. Brocklehurst." It appears that the grey squirrels increased steadily until his death in 1918, and before the death of Mr. W. W. Brocklehurst they became so troublesome that he gave orders to kill them down, "which order his son Mr. W. A. Brocklehurst in turn more heartily backed up. They had however got a very strong hold" (2). Also at Dunham Park, Cheshire, grey squirrels were present before the known introduction about 1911. They are stated to have been introduced there about 50 years ago (2).

The most important stock of American grey squirrels was brought to this country in 1889 by Mr. G. S. Page, of New Jersey. Five were released in Bushey Park, Middlesex, in 1890 (3, 4), but apparently failed to obtain a footing, as none were seen in Bushey Park until about the beginning of the present century. About ten were put down at Woburn Park, Bedfordshire (5), in the same year, 1890 (4), and there increased rapidly.

A little later a pair are reported to have been turned down at Finnart, on Loch Long, Scotland (3), but it is not known whether these came from the same stock brought over by Mr. Page. For the next ten or twelve years no further introductions appear to have been made, but during this period the stocks at Woburn and Loch Long were presumably increasing in numbers and beginning to extend their range.

About 1902, or a little later, a quite independent introduction is reported at Kingston Hill, Surrey, when an American gentleman released a large number of grey squirrels from a collection brought over with him (6). As the house taken by this gentleman backed on to Richmond Park, it seems probable that these squirrels were released into the park, or in any event made it their primary home. From this date onwards, after they had become numerous at Woburn, a wave of introductions took place in all parts of the country, most of the squirrels being obtained from the plentiful supply at Woburn, but others being introduced quite independently from America. It is unfortunate that no record was kept at Woburn of the squirrels sent to other parts of the country, as such a record would have made the task of tracing these secondary introductions a much easier matter than it has been found to be. In Table I. all the introductions of grey squirrels into the British Isles since 1889 of which evidence has been obtained up to the date of writing are summarised.

TABLE I. (For Map 1.)

Introductions of Grey Squirrels into the British Isles, 1889–1930.

No.	Locality.	Date.	Source.	No. introd.	Result.	Source of Information.
1.	Bushey, Middlesex ..	1889	U.S.A.	5	Died out.	3, 4
2.	Woburn, Bedford ..	1890	U.S.A.	10	Increased.	4, 5
3.	Loch Long, Scotland..	1892	..	2	Increased.	3
4.	Richmond, Surrey ..	1902	U.S.A.	100	Increased.	6
5.	Rossett, Denbigh ..	1903	Woburn	5	Increased.	7
6.	Lyme, Cheshire ..	1903–04	..	25	Increased.	2
7.	Regents Park, London	1905	Woburn.	5	Increased.	8
	,, ,, ,,	1906	Woburn.	36		
	,, ,, ,,	1907	Woburn.	50		
8.	Scampston Hall, Yorks	1906	Woburn.	36	Increased.	9
9.	Kew Gardens, London	1908	Woburn.	4	Increased.	3
10.	Cliveden, Bucks ..	..	..	2	Increased.	10
11.	Farnham Royal, Bucks	1908	U.S.A.	..		11
12.	,, ,, ,,	1909	U.S.A.	5		11
13.	,, ,, ,,	1909	S. Africa.	1		11
14.	Dunham, Cheshire ..	1910	..	2	Increased.	2
15.	Frimley, Surrey ..	1910	U.S.A.	8	Increased.	12
16.	Sandling, Kent ..	1910	..	..	Increased.	13
17.	Near Chiddingstone, Kent.	..	..	..	Increased.	13
18.	Benenden, Kent ..	..	..	..	Increased.	13
19.	Bramhall, Cheshire ..	1911–12	Woburn.	5	Uncertain.	2
20.	Birmingham	1912	..	..	Increased.	14
21.	Castle Forbes, Ireland	1913	Woburn.	8	Increased.	15
22.	Near Bedale, Yorks ..	1913	..	..	Increased.	16, 17
23.	Nuneham, Oxon ..	..	..	..	Increased.	3, 18
24.	Bingley, W. Yorks ..	1914	..	14	Slight increase.	19
25.	Exeter, Devon ..	1915	..	4	Increased.	3
26.	Stanwick, Northants..	1918	..	2	Increased.	20
27.	Dunfermline, Fife ..	1919	..	..	Increased.	21
28.	Edinburgh	..	Zool. Gdns.	..	Occasional.	22
29.	Bournemouth, Hants	Before 1922.	London.	6	Increased.	23, 3
30.	Hebden Bridge, W. Yorks.	1921	..	6 or 8	Slight increase.	24
31.	Needwood Forest, Staffs.	1929	Bournemouth	2	Alive 1930.	25, 23
32.	Northrepps, Norfolk	..	..	..	..	3
33.	Ayrshire	..	..	..	..	3

It is difficult to estimate the relative importance of each of the introductions, owing to their number and the fact that, especially in Southern England and Cheshire, the extension from different centres has now considerably overlapped. In the case of such centres as Stanwick, Northants, Kew, and Birmingham the effect may have been merely to augment the population locally, as the spread from other areas would probably have covered the same ground—and almost certainly has done by 1930. In the region of Stanwick, for example, there are sure to be descendants of the directly introduced specimens and others which have spread into the district from Woburn. The same reasoning probably applies to many parts of South-East England, where five equally distributed centres have contributed to the present result.

Of the centres tabulated, several are of very little importance as regards the distribution up to date. In Yorkshire the main distribution is due to the Malton and Bedale centres, while those at Bingley and near Halifax appear to have made very little headway, although specimens are still in existence there. Up to the time of writing I have failed to trace the present existence of any squirrels derived from the Norfolk and Ayrshire centres. The Edinburgh centre,

up to the present, appears to consist only of occasional escapes from the Zoological Gardens at Corstophine, and no pronounced extension has been brought to my notice. The grey squirrels present in North Wales in 1828 have, so far as is known, no relation to any of the areas at present colonized in that region; in fact, no positive records have been obtained from Wales with the exception of the centre just over the border of Denbighshire near Wrexham.

In Map 1 (Pl. I.) the positions of all the centres given in the table are marked, the numbers corresponding to the numerical order of the table.

4. Spread and Distribution.

In Map 2 (Pl. II.) the general distribution of the grey squirrel in the British Isles by 1930 is shown, with the main centres of introduction marked. The total area covered up to date is approximately 13,350 square miles, the greater part of which is made up of South-East England, the Midlands, and Yorkshire.

In mapping out the spread of the grey squirrel since its first important introduction in 1890 it was found impracticable to construct any form of accurate contour-map which would show the progress made from year to year, as the great number of separate introductions at different dates, and the difficulty of obtaining accurate chronological data regarding both introductions and first appearances, make the spread and distribution an extremely complicated matter. In order to show as much detail as possible of the extension from different centres, separate maps have been constructed of the three main areas. Map 3 (Pl. III.) gives the South and Midlands, incorporating the distribution derived from the Woburn, London, and South-Eastern centres; Map 4 (Pl. IV.) shows the distribution in Yorkshire; and Map 5 (Pl. V.) includes the Cheshire and Denbighshire centres.

On these maps the introduction-points are marked, and dated where possible, and four symbols are used to show that the squirrels reached the localities marked—(*a*) before 1910, (*b*) before 1920, (*c*) before 1926, (*d*) before 1930. Other symbols are used to show localities where grey squirrels were known to be present in 1930, but where the date of arrival has not been ascertained. Negative evidence is not given for the whole of the remainder of the country; but there is ample evidence to show that the areas clear of the distribution given are not populated by grey squirrels, except for the possibility of a few solitary specimens. The date 1926 was chosen as one of the limits in order that some of the information contained in Dr. F. V. Theobald's Bulletin on the grey squirrel in Kent, Surrey, and Sussex (13) might be incorporated in the map of the South-Eastern area.

In Maps 3 and 4 thick red lines have been drawn round areas which were probably populated before 1920, and a dotted red line indicates the probable limits of the distribution in 1930. It must be understood, however, that these contours are not by any means accurate for any particular area, but are based on general conclusions drawn from the evidence of distribution.

A tabulated list of all the localities from which positive reports have been received is also given, with the date of first arrival, if known. Where more than one report has been received from the same locality only one is usually quoted in full; some of the localities tabulated are not marked on the maps when they are situated very near to others which are marked and no noticeable difference in the date of arrival is to be shown. As each item of information generally refers to a district, rather than to a definite point on the map, it may be taken that, where the symbols are not widely separated, the grey squirrel is present in most of the suitable situations in the marked areas.

Of the four separate introductions made in the neighbourhood of Farnham Royal and Cliveden, Buckinghamshire, it is impossible to say which were of the greatest significance, but the abundance of grey squirrels in that district and Burnham Beeches dates back at least to 1910, and it is therefore probable that these introductions are together mainly responsible for the numbers in that area.

It may be remarked that the single female grey squirrel from South Africa, which was released at Farnham Royal in 1909, was last seen in the company of a red male. This grey squirrel would probably be the American species, as they were introduced into South Africa by the late Cecil Rhodes, and became very numerous and troublesome there (30).

Tabulated evidence is given for those parts of the country not included in the maps. For the district of Dumbartonshire, in Scotland, it is regretted that recent information has not been obtained, and most of the references given are derived from literature, being mainly the observations of Mr. James Patterson.

TABLE II. (For Map 3.)

Distribution of Grey Squirrels in the British Isles by 1930.

Localities where present.	Date of arrival.	Source of information.
KENT.		
Sandling (introduced)	1910	13
Chiddingstone district (introduced)	? Before 1910	13
Benenden (introduced)	? Before 1905	13
Tunbridge Wells	1925	31, 32
Edenbridge	About 1915–18	33
Cranbrook	1905	34
Bickley	1916	35, 36
Southborough	Before 1927	37
Sevenoaks–Westerham	1913	38
Brasted	Before 1919	39, 40
Brenderley	1925	41
Lamberhurst		42
Lynsted	About 1914	43
Hayes	Before 1927	44
Fairhill, near Tonbridge	1918	45
Chatham	1929	46
Charing	Before 1925	47
Hawkhurst	Before 1924	48
Crockenhill	Before 1926	13
Malling	1919	13
Horton Kirby	Before 1926	13
Ruckinge	1921	13
Maidstone district	About 1920	13
Northfleet	Before 1926	13
Cobham		
Newington		
Chevening		
Fenshurst		
Boxley		
Hollingbourne		
Linton		
Marden		
Westwell		
Godmersham		
Smeeth		
Frittenden		
Goudhurst		
Biddenden		
Woodchurch		
Tenterden		
Elmsted		
SUSSEX.		
Ashurst	1924	49
High Hurst, Uckfield	1927	50
Robertsbridge	1915	51
Cross-in-Hand	1925–26	52, 53
Chichester district	Before 1930	54

Localities where present.	Date of arrival.	Source of information.
Five Ashes	1927	52
Fairlight, Hastings	1918	55
Framfield	1919	56
Northian-Bodiam	Before 1926	13
Crowhurst	1919	13
Eridge	1921	13
Hastings, parks	1920	57
Hollington	1908	57
Withyham	1909	34
Worth	1925	58
Dallington	1923	59
Horsham district	About 1915	3, 60
Nuthurst	1929	40
Kings Standing	Before 1928	61
Crawley Down	Before 1928	61
Lindfield	1919	61
Billinghurst	Before 1926	13
Wisboro'		
Ewhurst		
Ticehurst		
Tidebrook		
Wadhurst		
Battle		
Ashburnham		
Wartling		
Brightling		
Guestling		
Bayham		
London and Middlesex.		
Regent's Park (introduced)	1905	8
Hyde Park, etc.	About 1908	3
Hampton Court	1916	3
Bushey Park	1903	3
Kew Gardens (introduced)	1908	3
Twickenham	1914	3
Enfield	1928	62
Rickmansworth		63
Harefield, Uxbridge	1921	63
Whetstone	About 1929	64, 65
Edgware	1928	66
Hadley, near Barnet	Before 1930	67
Surrey.		
Richmond (introduced)	1902	6
Warlingham	1921	68
Arbrook	1918	13
Dorking	Before 1926	13, 69
Woolmer Forest	1926	70
Great Bookham	About 1924	71
Wisley	1925	13
Hambledon	1928	72
Caterham	About 1920	73, 3
Camberley	1914	74
Walton-on-Thames	1915	75
Nutfield	1929	76
Frimley (introduced)	1910	12
Tadworth	About 1920	77
Chiddingfold	Before 1929	78
Walton-Weybridge	Before 1921	79
Epsom		80
Guildford	1930	43
Leatherhead	About 1920	3
Ottershaw	Before 1924	82

Localities where present.	Date of arrival.	Source of information.
Roehampton	Before 1926	13
Surbiton		
Chessington		
Esher		
Cobham		
Chertsey		
Bagshot		
Woking		
Virginia Water		
Ockham		
Clandon		
Horsley		
Shere		
Albury		
Limpsfield		
Woldingham		
ESSEX.		
Stanway, near Colchester	1927	83
Wanstead Park	1917	84
WILTSHIRE.		
Savernake Forest	1925	85
Marlborough	1929	86
Salisbury	1928	87
HAMPSHIRE.		
Alresford	1927	88
Alton district	Before 1928	89, 90
Alton (West)	1930	91
Hartley Wintney	Before 1926	92
Andover	1929	93
Yately	1918	94
Basingstoke district	1919	95
Domersfield		96
Fleet	About 1926	97
Silchester, near Basingstoke		98
Hythe	1926	99
Bournemouth district (introduced)	Before 1922	3, 23
BERKSHIRE.		
Crowthorne	1924	100, 101
Reading, South-East	1923	102
Ascot district	1919	103
Tilehurst	1927	104
Finchampstead	1923	105
Suthampstead	1926	106
Upton Nervet	1929	106
Yattendon	1925	107
Ashampstead	Before 1929	107
Theale	Before 1929	107
Swallowfield	Before 1927	108
Buckland	Before 1928	108
Wargrave	1919	3
Windsor Park	About 1921	69
HERTFORDSHIRE.		
Kings Langley	1921	109
Ashbridge Park	1916	3
Bushey Heath	Before 1927	110
Little Berkhampstead	1926	111
Hitchin	1910	112

Localities where present.	Date of arrival.	Source of information.
Stevenage	..	113
Watford	1919	3
Berkhamsted	Before 1923	114
Tring	Before 1914	3
St. Albans	Before 1924	115
BUCKINGHAMSHIRE.		
Farnham Royal (introduced)	1908–09	11
Cliveden (introduced)	..	10
Stoke Poges	1916	116
High Wycombe	1916	117
Aylesbury district	Before 1910	3
Buckingham	Before 1923	3
Burnham Beeches	Before 1910	118
Newport Pagnell	1911	119
Brill	1923	120
Stowe	Before 1923	3
Wendover	1920	121
Ellesborough	1928	122
Gt. Missenden	..	122
Ivinghoe	Before 1923	3
Whaddon	Before 1923	3
OXFORDSHIRE.		
Nuneham–Sandford (introduced)	..	18, 3
Oxford district	Before 1913	18
Oxford City	About 1916	18
Marston	..	123
Bagley	..	123
Radley	..	123
Banbury district	1916	3
Harpsden, Henley	Before 1929	124
Charlbury	1917	125
Chipping Norton	..	108
Sibford Finis	Before 1928	126
Heythrope	Before 1930	127
Kingham	Before 1929	127
Deddington	Before 1929	128
Burford	1925	108
Hailey	Before 1929	108
Glympton	Before 1929	129
Woodstock	Before 1929	123
Wyfold Court	1928	130
BEDFORDSHIRE.		
Generally over the whole county	Before 1923	3
Turvey	1912	131
Woburn (introduced)	1890	5
Leighton Buzzard	..	132
NORTHAMPTONSHIRE.		
Northampton district	1920	134
Preston Capes	1918	133
Stanwick (introduced)	1918	20
Syresham	1915	135
Daventry district	1915	136
Piddington	1915	137
Weston	About 1912	138, 123
Castle Ashby	Before 1920	3
Wellingborough–Oundle	1920–30	20
Raunds district	About 1920	20

Localities where present.	Date of arrival.	Source of information.
Warwickshire.		
Brailes	Before 1929	139
Birmingham (introduced)	1912	14
Birmingham district	About 1925	140, 141
Alcester district	1924–25	142
Princethorpe	1918	143
Kenilworth	1921	144
Coventry district	1926	145, 149
Warley	Before 1928	146
Bourneville	1928	147
Coleshill	1929	148
Carling	..	149
Gloucestershire.		
Cheltenham district	1921	150
Stonehouse	1929	151
Huntingdonshire.		
Buckden	..	2
Brampton	..	2
Cambridgeshire.		
Occasional near borders of Bedfordshire	Before 1923	3

Table III. (For Map 4.)

Distribution in the Yorkshire Area.

Localities where present.	Date of arrival.	Source of information.
Scampston, near Malton (introduced)	1906	9
Bedale (introduced)	1913	16, 17
Helmsley	1913	152
Kingthorpe	..	153
Castle Howard	Before 1920	154
Moreby Escrick	1914	135
Settle	1929	108
Ellington, Masham	..	156
Ripon	1920	157
Upper Wharfedale	..	158
Keighley	1924	159
Jervaulx	Before 1926	160
Thornton Dale	Before 1920	161
Ilkley	1922	162, 3
Barden	1928	163
Ampleforth	..	164
Sand Hutton	1909	165
Sutton-on-Derwent	1926	166
York district	About 1922–23	167
Gilling	1913	168
Near Whitby	Before 1929	153
Kirklington	Before 1924	163
Guisley	1927	169
Conwold	..	169
Rainoliffe	1929	170
Simmington	1930	170
Hackness	Before 1929	170
Scalby	1930	170
Marton-in-Cleveland	1927	171
Ingleby	About 1925	171
Meanwood, Leeds	1930	172
Kirkby Underdale	Before 1923	173
Selby	About 1926	174

Localities where present.	Date of arrival.	Source of information.
Near Gainford, Durham	1929	175
Leyburn	1928	176
Ribston	About 1926	177
Scorton		178
Haughton, Newbald	1926	179
Northallerton district	Before 1920	180
Bingley (introduced)	1914	19
Hardcastle, Hebden Bridge (introduced)	1921	24
Plumpton	1923	17

TABLE IV. (For Map 5.)

Distribution in the Cheshire Area and North Wales.

Localities where present.	Date of arrival.	Source of information.
Henbury (introduced)	1876	2
Dunham (introduced)	About 1880	2
Dunham (introduced)	1910	2, 181
Bramhall (introduced)	1911–12	2, 181
Lyme (introduced)	1903–04	2
Disley	Before 1910	2
Alderley Edge	1911–12	2, 181
Adlington Hall	1904	2
Eaton, Congleton	1913	2
Mottram	1919	2
Crag Hall	1928	2
Withington Hall	About 1910	2
Astle	About 1919	2
Erwood	1914	2
Goyt Valley	1914	2
Poynton	Before 1915	2
Swythamley	1924	2
Hare Hill	1911	2
Birtles	1918	2
Endon Hall	..	2
Upton	1920	2, 182
Toft	1920	2
Thorneycroft	1914	2
Capesthorn	..	2
Kermisham	..	2
Jodrell	..	2
Ladsham	1929	182
Claughton	1929	182
Bowdon	1911	181
Tatton	Before 1924	181
Mobberley	1922–23	181
Rostherne	1922–23	181
Withington (Lancs)	1916	181
Chelford	1911	183
Gawsworth	1926	2
Brereton	1922	2
Norton, near Warrington	..	2
Barleighford	..	2
Moreton	1914	2
Rode Heath	Before 1920	2
Rossett, Denbigh (introduced)	1902–03	7
Eaton Park	1905	7
Marchweil	1928	184
Bryn-y-Grog	Before 1930	184
Chirk		2
Oswestry	1928	2

TABLE V.

Distribution in Scotland.

Localities where present.	Date of arrival.	Source of information.
DUMBARTONSHIRE AREA.		
Finnart (introduced)	About 1892	3, 22
Arrochar	1903	185
Tarbert	1903	185
Luss	1904	185
Inverbeg	1906	185
Gareloch-head	1907	185
Arnburn	1908	185
Alexandria	1912	185
Culdross	1912	185
Camiseskan	1912	185
Row	1912	185
Roseneath	1915	22
Drymen	1915	22
Touch, Stirling	..	21
DUNFERMLINE AREA.		
Pittencrieff Park (set free)	1919	21
Pitfirn	Before 1923	21
Rosyth	Before 1923	21
Invergowrie, Dundee	1929	—
Pitfirrane	About 1927	271
EDINBURGH AREA.		
Corstophine (escaped)	About 1913	3
Dalmeny Park	About 1919	22
Edinburgh outskirts	1927	186
AYRSHIRE.		
No reports, 1930.		
Brisbane, Largs	1919	3
Montgreenan	Before 1923	3
Eglington	Before 1923	3

TABLE VI.

Distribution in other Areas.

Centre.	Present Distribution.	Source of information.
Co. Longford, Ireland ..	Spread to within a few miles radius of Newtownforbes, but said to be kept under control.	15
Exeter	District of Exeter, and up the Exe Valley about 6 miles north of Exeter.	123, 3, 187
Bournemouth	Throughout gardens and environs of the town ..	3, 188, 23
Northrepps, Norfolk ..	No records received since before 1923	123, 3, 189, 190
Nottinghamshire ..	Present in woods, Bestwood and Hartsholme, north of Nottingham, 1929.	26
"	Wollaton Park	191

The way in which grey squirrels appear suddenly several miles from any previously populated locality, the difficulty of obtaining accurate information as to dates of first appearances, and the possibility of there being other points of introduction besides those already ascertained, make it difficult to trace the

spread and increase in detail. But, generally speaking, the evidence available indicates that the grey squirrel is more inclined to follow the course of a valley than to extend on to higher ground, even though the high ground may be profusely wooded. There are very few hills of any significance in the area of England occupied by these squirrels up to date, but it may be remarked that from the tops of the profusely wooded Chilterns no records have been received, although in the neighbouring lowlands and valleys they have been plentiful for a considerable time. H. Boyd Watt, in a paper in the 'Essex Naturalist' in 1923, also remarks on this point, saying that in frequent rambles on the Chiltern Hills he had never seen a grey squirrel, although the conditions there appear to be ideal for them (3). As will be seen from the map of the Yorkshire area, the high ground forms a definite barrier to their distribution, which is in nearly all cases confined to the lower ground and river-valleys. Most of the hill-ground in Yorkshire, however, is moorland, with patches of woodland only at intervals, so that the population of such country would not be so easy as in the case of the Chilterns.

It appears quite certain that the extension of range is not due to over-population in areas already occupied. For example, in Wharfedale, Yorkshire, a rapid extension of range has been going on for the past seven or eight years, and a solitary specimen was seen as far west as Settle in 1929 (108); but the numbers present in Lower Wharfedale, where they have been present for at least five years, are still remarkably small (158), so that only one or two are occasionally seen. In this instance an extension of at least 35 miles has occurred with very little concentration in any locality. A similar state of affairs appears to exist in the Kennet Valley, west of Reading: the advance up the valley began from the district south of Reading soon after 1920, and by 1925 they had reached Savernake Forest (85). Some of the districts at the eastern end of the Kennet Valley, however, remained free until 1928 or 1929, while the numbers west of Reading on this route are negligible at the present time.

On the other hand, many favourable situations, such as Burnham Beeches, Bucks (118), Wychwood Forest, Oxon (125), and Thornton Dale, Yorks (161), have become veritable strongholds for grey squirrels, where the numbers appear to increase and remain to a great extent confined to the particular district. In an area of 500 acres at Burnham Beeches 4270 grey squirrels were killed in the ten years ending April 1930; and in Wychwood Forest, an area of 1400 acres, 3586 were killed in the four years ending December 1929. The annual kills for these areas are given below (the year at Burnham Beeches is from May 1st to April 30th):—

Year.	Burnham.	Wychwood.
1921	300	—
1922	168	—
1923	514	—
1924	421	—
1925	275	—
1926	700	329
1927	303	742
1928	218	994
1929	1011	1521
1930	360	—

The figures for 1929 represent in Burnham Beeches a kill of approximately 2 per acre, and in Wychwood of 1 per acre, and assuming even that three quarters of the total number were killed, this would mean an average density of 3 per acre in the former area and 1·5 per acre in the latter.

It is interesting to compare these figures with similar records of red squirrels shot on Scottish estates. At Beaufort, Inverness, one of the worst afflicted areas, the figures in the plague year of 1907 show that only one squirrel was shot per five acres, which, calculated on the same basis, gives a concentration of about ·3 per acre.

Extensive migrations of grey squirrels in vast hordes have frequently been witnessed in America (192), but no mass migrations have so far been recorded in this country. There does, however, appear to be a strong migratory instinct among individuals rather than masses, as evidenced by the rapid extension of range carried out in thinly populated areas such as Wharfedale. It is possible that in this country the migratory instinct may be stronger in some individuals or families than in others, in which case the ones less inclined for migration would, by breeding, establish concentrated colonies, while the migratory ones were engaged in extending the range of the species. In the circumstances under which the spread of the grey squirrel has occurred in this country, where the population of large areas must in many cases have resulted from the progeny of isolated pairs, the genetical character of the ancestral individuals must have a pronounced influence on the character of the descendants, so that there is a much greater chance of certain variant characters becoming established in these circumstances than in the normal conditions of a constant population.

5. Habitats.

Practically all the areas where the grey squirrel has become exceeding numerous are open woodlands or park-lands with deciduous trees, and beech or mixed deciduous-conifer woods. In no case does it seem to take to the dense coniferous woods, which are the ideal habitat of the red squirrel. In America the grey squirrel is found mostly to the south of the big coniferous belts, in the deciduous forest zone, whereas the red squirrel is the typical northern conifer forest type. In the present range of the grey squirrel in this country there are very few large coniferous tracts, so that no definite decision can be arrived at on this point. But by the time the grey squirrel has completely populated this country there should be some coniferous forests of considerable extent, arising from the afforestation carried on during the last ten years, so that a very interesting field for the study of distinctive habitats will then be available. At the present time the only common habitat for any squirrel is scattered patches of mixed woodland, linked up by hedgerows, isolated trees, gardens, and park-lands, and in this habitat grey squirrels appear to live favourably enough.

They do not seem to avoid human habitations in any way so long as there are plenty of trees about, but there is no reason to suppose that grey squirrels are particularly inclined to associate with mankind. The number of half-tame squirrels to be seen in parks and pleasure gardens in no way reflects on the character of their country cousins.

6. Habits

The grey squirrel is extremely agile and active in the tree-tops, but undoubtedly spends a great deal of time on the ground, as it has frequently been observed several hundred yards from trees, apparently searching for bulbs and corms. When disturbed in a wood it will often run a hundred yards or more along the ground instead of taking to the nearest tree, as does the red squirrel. I have frequently found them in hedgerows quite a mile from any woods. Gamekeepers often catch them in traps set at the mouth of rabbit-burrows, and several instances are recorded of grey squirrels entering rabbit burrows when disturbed; they have also been bolted from rabbit-holes during ferreting operations.

The grey squirrel appears to make several dreys, but it is not known whether more than one is in use at the same time. It is probable that fresh dreys are made at intervals and the old ones deserted, which would account for the excessive number of dreys to be seen in woods favoured by the grey squirrel, most of them being uninhabited. In Wychwood Forest an estimate made from actual counts shows that in many parts there are at least 18 dreys to the acre, most of which are old and vacant. The dreys in this district are lodged in beech, oak, sycamore, and blackthorn, some in loose outlying branches and others solidly built in the forks of large trees. The materials used for building seem to vary with the dominant trees in the immediate locality; those in oak-trees are invariably built almost entirely of oak-leaves and twigs, while in beech-trees the beech-leaves and twigs are utilized. Some in isolated trees in open grassy glades are constructed almost entirely of long grasses and moss. One drey carefully examined, which was constructed in the fork of two main branches off the trunk of a large beech-tree, about 18 feet from the ground, was spherical in shape, completely covered at the top, with two entrances at the sides, about 20 inches over-all diameter. The stout base was formed of beech-twigs, covered by a thick layer of beech-leaves, grass, and moss. The whole was roofed over with a mixture of grass and beech leaves, interspersed with a few small beech-twigs; the central cavity was no more than 9 inches in diameter. This particular tree stood on the edge of a grassy ride in the wood, so that plenty of grass and moss could be obtained within 10 yards of the tree. They have also been seen using the bark stripped from fir-trees for making dreys (74). The breeding-nests appear to be built in hollow trees for preference, but when no such sites are available nests of the above description are made for this purpose.

An observant naturalist informs me that it is quite easy to distinguish the dreys of grey squirrels from those of the red species, as the former invariably use twigs with the leaves growing on them, while the latter always use dead twigs (18). I have not been able to verify this myself, but if such is the case a distinction of this kind would be of great value in taking censuses of dreys of the two species, and also for work on parasites, scavengers, etc., when it is often necessary to know the origin of a nest without the opportunity of seeing the owner.

A grey squirrel was seen to jump from a tree on to the back of a cock pheasant, much to the alarm of the pheasant (180), while another was seen chasing a young wood-pigeon which was unable to fly (108). They appear to possess good powers of scent. I watched a grey squirrel running in the tree-tops and along the ground through a wood for about a hundred yards; a few minutes later one appeared from the same direction, and followed the first one's course in every detail, running up the same sides of particular trees, along the same branches, and over the same stretch of ground as the animal he appeared to be following, although the first squirrel had disappeared from sight before the second one appeared.

Another grey squirrel was seen to gnaw a hole in an attaché case strapped to the back of a workman's bicycle and eat the man's lunch, which was contained therein (68). Discovering that a Cheshire gardener stored corn in his wash-house, grey squirrels "attacked the window-frames and tore the wood down to the glass, and when they got through the open door on one occasion they nearly ate their way out through the same window before discovery" (2).

Many gamekeepers complain of the grey squirrel's cleverness in avoiding the effects of a shot-gun by carefully keeping on the opposite side of the tree to the keeper. Where pheasants are hand-fed with corn, the squirrels frequently run down among the pheasants to feed in front of the keeper, who is unable to shoot at them in such circumstances. They have also learnt to work patent pheasant-

feeders with their fore paws, in order to tip out the contents on to the ground (78).

Like other rodents, the grey squirrel is obliged to exercise its teeth a great deal, by gnawing hard substances such as the bark of trees, in order to prevent them growing to an uncomfortable length. One which was kept as a pet by the late E. J. Harting grew such enormous incisors that it was unable to feed properly, and had to be destroyed (4).

Numerous observations of pure albino grey squirrels have been reported practically all from the South-Eastern district of England. No example of melanism has yet been brought to my attention.

7. Breeding.

Little is known at present about the reproduction of grey squirrels in this country, but I have recently started an investigation into this subject, with the help of unique facilities given by Mr. O. Watney in sending me a regular monthly quota of squirrels for examination from Wychwood Forest, which it is hoped will throw some light on the facts of their breeding powers and other points. It may be mentioned that 23 females examined during March and April 1930 showed no signs of pregnancy nor the beginning of sexual activity, although most of the males examined were in a sexually active condition.

There are records of five young found in a nest (194), and a nest with four young (Scotland) in April 1927 (195). In America the grey squirrel is stated to have four to six young in a litter (29). The earliest record of young found in the nest in the Oxford district is May 6th (18).

8. Food and Damage.

As the main body of the evidence on which this paper is based has been obtained from the observations of a large number of correspondents, many diverse views are found to exist regarding the food of the grey squirrel. If stress were laid upon the individual observations of people with rather different view-points it wold appear that in some districts the grey squirrel exists entirely on the eggs and young of pheasants, while in others it would appear to eat nothing but unripe walnuts. In order to neutralise the errors of this kind, two lists have been constructed showing all the common ingredients of the grey squirrel's diet, classified under plant and animal headings. The items listed have all been observed to be eaten by the squirrels, and a large amount of general information has been neglected where it was not backed up by first-hand observation.

As far as can be ascertained there is no noticeable geographical variation in the types of food eaten, though of course there is considerable local variation dependent on the relative amounts of different foods available. After examination of this list it would appear difficult to state what is the most important and usual food of the grey squirrel, and one is inclined to agree with the assertion of one of my correspondents that, "like rats, they will eat anything." The food must vary a great deal seasonally and with the particular environment of the animals. Squirrels living in a woodland area are compelled to make up their diet from shoots and bark of trees, bulbs, nuts, seeds, such wild fruits as are available, and in the nesting season an occasional feed of eggs or young birds, with, perhaps, a young rabbit stolen from a nest, if the squirrel is able and fortunate enough to carry out such a raid in safety. There is little doubt that green food, fruit, and nuts form the major part of the food supply of most grey squirrels, but there is also no doubt that these rodents are frequent robbers of birds' nests.

TABLE VII.

Food of the Grey Squirrel.

Plant Life.	Eggs.	Animal Life.
Spruce shoots.	Rook.	Rabbits.
Larch shoots.	Blackbird.	Blackbirds, young.
Douglas fir shoots.	Song-Thrush.	Thrush, young.
Beech shoots.	Mistle-Thrush.	Blue-Tit, adult.
Scots pine shoots.	Starling.	Jay, young.
Chestnut buds.	Rock-Pigeon.	Chaffinch, young.
Cherry buds.	Wood-Pigeon.	Pheasant, young.
Sycamore bark.	Nightingale.	Partridge, young.
Beech bark.	Woodpecker.	Domestic chickens.
Chestnut bark.	Nuthatch.	
Magnolia.	Kestrel.	
Rhododendrons.	Bullfinch.	
Bulbs	Pheasant.	
Peas.	Partridge.	
Grapes.	Domestic fowls.	
Plums.		
Apples.		
Cherries.		
Peaches.		
Figs.		
Pears.		
Loganberries.		
Gooseberris.		
Strawberries.		
Raspberries.		
Tomatoes.		
Hazel nuts.		
Acorns.		
Beech mast.		
Maize.		
Horse chestnuts.		
Spanish chestnuts.		
Walnuts.		
Filberts.		
Pine seeds.		
Larch seeds		
Corn, from stores.		
Wheat, growing.		

At present it is difficult to give any accurate representation of the extent to which the grey squirrel robs birds' nests, but there is no doubt that the eggs and young of the birds listed have frequently been taken by them. It is probable, however, that egg-eating is more an individual habit than a general one, for if all grey squirrels were as eager to eat birds' eggs and young as many people seem to believe, there would not be a bird left in many of its present strongholds. It is difficult to imagine any animal more suited for the practice of robbing nests than the squirrel, and if eggs were a much-sought-after food the nests of practically all the common birds could be raided with the greatest of ease. In such an area as Wychwood Forest there is no reason why the grey squirrel could not exterminate the entire resident bird population in the course of one breeding season. But the enormous squirrel population of Wychwood does not appear to have reduced the birds to any noticeable extent. It is possible that the destruction of eggs is mainly the work of "rogue" squirrels which have acquired a particular taste for them.

If, however, as seems to be the case, the habit of nest-robbing is occasional, and generally dependent on the chance of squirrels finding nests in the course of their regular wanderings, then it is probable that the birds to suffer most will be the smaller species, which are unable to defend their nests against a squirrel, and

game-birds, whose nests are often left unprotected at the slightest cause for alarm. Both these aspects are of importance to the ornithologist, and the former is likely to prove of more serious economic interest in its indirect effects, owing to the fact that many of the most susceptible birds are insectivorous, and any great reduction in their numbers may be reflected in an increase in the insects upon which they normally feed. Strangely enough, the destruction of game-birds' eggs has evoked greater consternation than the more far-reaching destruction of insect-eating birds.

The method employed in eating a pheasant's egg has been carefully watched by a reliable observer, and is worth recording here. The grey squirrel took the egg in its fore paws and nibbled a hole in the shell of the pointed end. The contents of the egg were then sucked out, the squirrel being observed at intervals to tilt its head and swallow the liquid with great enjoyment. Seven out of ten eggs from a nest in Bagley Wood, near Oxford, were eaten in this way by the same squirrel (18).

Their offences against the gamekeeper appear to lie in more than one direction, as by collecting and eating beech-mast they are said to rob pheasants of a valuable natural food (193). They gnaw holes in wooden feeding-boxes to extract the corn, and on one estate in Yorkshire it has been found necessary to substitute metal feeders for the wooden ones (161). When pheasants are being taken in for breeding purposes grey squirrels are frequently taken in the traps. In the spring of 1929, at Birtles Hall, Cheshire, 32 box-traps were set for pheasants, and the first day's catch was 25 grey squirrels; when caught in these traps they often gnaw holes through the wood and make their escape (2). Grey squirrels have been accused of robbing the nests of rooks and causing desertion of the rookeries (196). Birds have been seen mobbing grey squirrels in the same manner as they do owls and hawks (71).

Many instances are recorded of young rabbits being killed and eaten, and in one case a grey squirrel is said to have killed a mature rabbit by biting it at the back of the head in the manner of a stoat (197). Several squirrels have been seen together making a meal off a dead rabbit (136), while a young rabbit laid open near a trap is said to be an infallible bait for them (2). They are often caught in traps set and baited for stoats with flesh, eggs, etc. A rather amusing incident is recounted from an estate in Cheshire:—"Some little time ago there were rats about the hen pens, so he (the keeper) put strychnine on two hen carcases and placed one under the cote and one in the open. Next day he found three dead rats and a live grey squirrel chewing a hen carcase (2)."

Several reliable instances of grey squirrels taking hens' eggs are recorded, and one particularly striking one occurred on a poultry farm in Cheshire—though this case is not quite conclusive in itself. "There were 500 head of poultry, and shortly the egg supply ran low. Rats were suggested, but one day their terrier barked at a fallen tree, and when it was moved by the help of a crowbar a grey squirrel ran out and was promptly killed by the dog. Over 200 hens' eggs were found stored below" (2). In the same area disused rabbit-holes have been found packed tightly with chestnuts, acorns, and beech-mast (2).

In so far as "eating" is almost synonymous with "damaging" in this country, it must be admitted that the grey squirrel does a great deal of damage to many kinds of trees, fruits, and plants. From the forestry point of view serious damage is done by peeling or "ringing" the bark of young trees, in which respect sycamores and beeches appear to be the most affected. In Wychwood Forest hundreds of sycamores and beeches of about 10–20 years' growth have been killed by this practice of peeling patches of the entire sap-bearing inner bark (115), and at Scampston Hall, Yorks, similar damage has been experienced, mainly in sycamores (9). In Burnham Beeches the bark of young branches of the beeches has been treated in the same fashion (118). Another serious form of damage affecting forestry is the biting off of the shoots and leaders of young

conifers. Buds and fresh green shoots of most trees certainly form a very palatable food for squirrels of all kinds, and when the trees affected are part of an afforestation scheme, or happen to be fruit-trees, squirrels must be regarded as frustrating human efforts, and consequently a "pest."

Fruits and nuts of most kinds appear to be eaten with avidity, and many complaints have been received of the way in which grey squirrels strip trees of walnuts, hazel nuts, etc., before the nuts are ripe. The grey squirrel also appears to be frequently addicted to the practice of biting off ears of growing corn, and has been found taking corn in quantities both from corn-stacks and stores. A Cheshire head gardener was under the impression that his men were stealing tomatoes from the glass houses until, after a period of watching, he discovered that grey squirrels were entering through the ventilators and removing the tomatoes. The tomatoes were found collected into neat piles in some long grass nearby, and had not been damaged in any way by the squirrels in the process of removal (2).

Mushrooms and other fungi are frequently eaten by grey squirrels in America (198). I have no records of this from the British Isles, but it is probable that fungi are eaten when the opportunity occurs.

9. Enemies and Parasites.

The grey squirrel does not appear to have any natural enemies of consequence in this country with the exception of man, and possibly disease. Man is, of course, a very formidable enemy in such areas as he chooses to exert his influence, as the two examples of shooting records already cited will show; but, judging by appearances, even such intensive shooting as this does not prevent an increase in numbers or keep them down to a reasonable level.

The parasites of the grey squirrel do not appear to have been thoroughly worked out in this country, but it is known to have a special flea, *Ceratophyllus wickhami*, which has been found in large numbers in Buckinghamshire (199). I have recently started a routine examination of the parasitic fauna of a monthly quota of grey squirrels from Wychwood Forest, Oxon, and the fleas obtained from 56 grey squirrels examined during March–May 1930 up to the time of writing are:—

66 *Ceratophyllus sciurorum* Lebrank.
6 *Spilopsyllus cuniculi* Dale.
3 *Ceratophyllus gallinæ* Lebrank.

I am indebted to Mr. F. J. Cox for the identification of these fleas.

It is interesting to note that no specimens of the true grey-squirrel flea, *Ceratophyllus wickhami*, are among these fleas collected from the Wychwood squirrels.

10. Seasonal Activity.

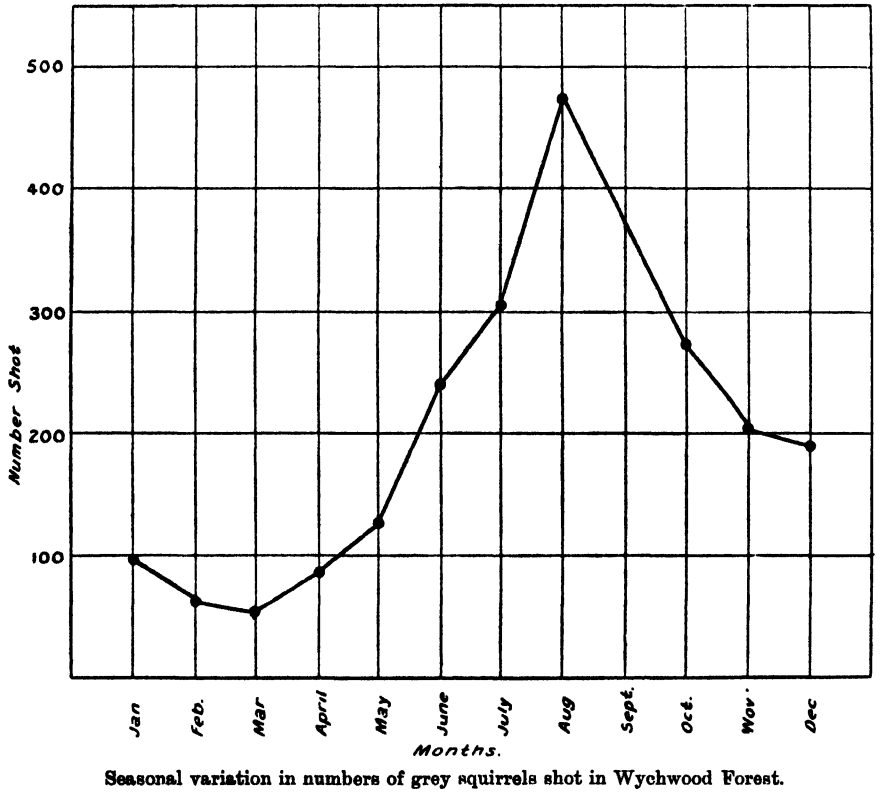
There is little doubt that the grey squirrel remains active throughout the whole year, and does not hibernate in the true sense of the word. There is, however, considerably less activity during the winter months than in the summer, and it is probable that the grey squirrel sleeps most of the time during severe weather. The number shot in Wychwood Forest varies considerably at different seasons of the year. The following are the monthly figures for 1928 and 1929 for this area:—

January	52	41	101
February.....	35	27	33
March	32	27	25
April	36	52	—

May	46	77	—
June	105	138	—
July	174	127	—
August	162	313	—
September	128	267	—
October	75	200	—
November	81	121	—
December	68	131	—

In text-fig. 1 a graph is given of this monthly variation in the numbers shot, the average of the two years being taken. The extreme peak in August is probably due in a large measure to the number of young then about in the woods, but it must be noted that during the winter there is a much greater chance of the keepers shooting squirrels, as they are more easily seen in the absence of dense foliage; also

Text-figure 1.



Seasonal variation in numbers of grey squirrels shot in Wychwood Forest.
(Data for 1928 and 1929 combined.)

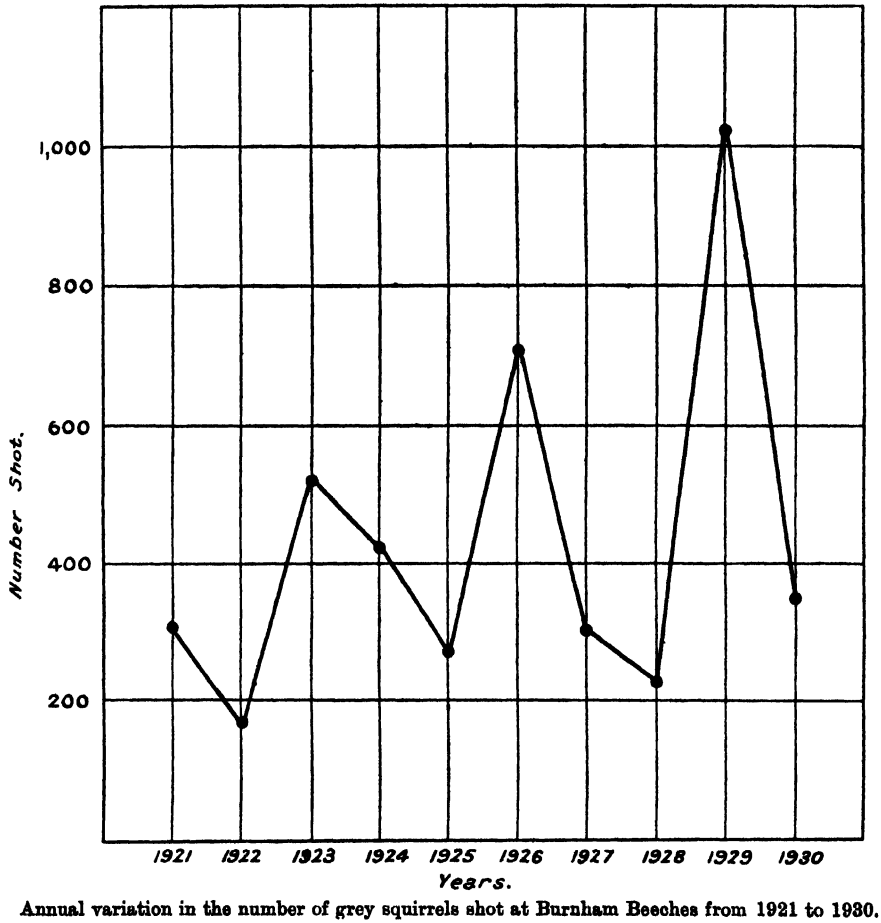
general shooting is less prevalent in the summer than in the winter months. It appears certain from this curve that there is much more general activity among the squirrels in the summer than in the winter, which is only to be expected.

They have repeatedly been seen running about on snow, and on almost any fine day during the winter some may be found active.

11. Fluctuations and Disease.

Generally speaking, the grey squirrel has not been in occupation of this country for a sufficiently long period to show any marked fluctuation in numbers. At Burnham Beeches, however, a series of observations and shooting records are available which show that there has been a considerable variation in the numbers present in different years. For some years up to 1918 they were very abundant, but in 1919 a great reduction in numbers was noticed, and many were found dead

Text-figure 2.



Annual variation in the number of grey squirrels shot at Burnham Beeches from 1921 to 1930.

with symptoms of "mange" (200, 201). In 1920 regular shooting of grey squirrels was started by the gamekeepers, the records of which have already been given. In text-fig. 2 the records of the numbers shot since 1920 are shown in the form of a graph. There is every reason to believe that the shooting throughout this period was fairly constant, so that the fluctuations shown, which in some cases show a difference of five to one, are probably reflections of a varying population rather than a variation in the keeper's activity. It will be interesting to see if the apparent three-year periodicity is a real one.

Near Cranbrook, Kent (another area where grey squirrels have been present for a considerable period), great numbers were found dead from some disease in 1923–24, and the numbers were much reduced for a time in that district (13). At Henbury Park, Cheshire, in 1925, a disease killed off large numbers; the squirrels were noticed to have fur off in patches, scrofulous skins, and "tails like rats" (2). On the Castle Howard estate, North Yorkshire, grey squirrels were very numerous for a period up to 1922, but about that time a great reduction in numbers occurred, and in 1929 they were reported as scarce (154). At Gilling Castle, a few miles from Castle Howard, they were very numerous about 1920, but by 1929 were reported to have decreased considerably in numbers (168). Also at Ellington, Yorkshire, they were reported in 1929–30 to be "not so numerous as a few years ago" (156).

In the Weston district, South Northamptonshire, grey squirrels were very numerous by about 1920, but from 1926–30 were noticeably less numerous. At Oxford they were common in college gardens and in the parks about 1918–24, but few were seen from 1926–29, and at the time of writing (May 1930) none are to be seen in the neighbourhood of the parks and college gardens, and few on the outskirts of the city (123).

Although it is possible that some of these instances may be explained by local migrations into more favourable areas, it would appear that in some areas where the grey squirrel has been established for a long time there are signs of the beginning of natural fluctuations in numbers, in some cases associated with outbreaks of disease, as is known to be the case with many other rodents, such as field-voles in this country (202), lemming and squirrels in Scandinavia, and rabbits and fur-bearing animals in Canada (203). It is only to be expected that the grey squirrel will respond to the as yet unexplained cycles of increase and scarcity which are so pronounced in other animals throughout the world.

It may be of interest to mention here the case of the island of Motuna, 40 miles off the coast of New Zealand, which was stocked with rabbits about 1860. Before 1890 a natural cycle in numbers had come into force, controlled by epidemics of disease at regular intervals of seven years (204).

12. Economic Importance and Control Measures.

In a highly cultivated country like Great Britain the support of an additional rodent is bound to be of considerable economic significance if its numbers become at all large. The progress made by the grey squirrel up to the present time, and the high population present in particular areas, leaves little room for doubt that it will eventually become distributed throughout the country. When the process of colonization of new areas has reached its limit, it is probable that grey squirrels will become as abundant over the greater part of the country as they are in a few localities at present. From the squirrel's point of view the nature of the country will have undergone a remarkable change by the time it has spread into every corner of the British Isles: there will be at least 750,000 acres of additional woodland as a result of the afforestation now going on; agriculture will probably be of a more intensive nature, and therefore more susceptible to rodent damage, and a considerable increase in fruit-growing is to be expected. This country will then be able to support a far larger squirrel population than it can do at the moment—the period about 1950 onwards will, in fact, be an age of prosperity for squirrels if they are allowed to follow their natural inclinations. But the increased areas of forest are being raised as a commercial undertaking, and consequently the toll which squirrels are bound to levy will become of direct financial importance to the country. The enormous damage done to the coniferous forests of Scotland by the red squirrel is well known, and there is every reason to believe that the grey squirrel would become quite as formidable a pest as the native species, and a less specialized one.

It is difficult to say at present what will be the most serious offence of the grey squirrel from an economic standpoint, but it is probable that in the long run the destruction of bird-life will be of the greatest importance to both forestry and agriculture. The direct destruction of marketable produce must also assume considerable dimensions if a heavy grey squirrel population becomes generally distributed. The wide range of food-stuffs eaten by the grey squirrel would make it a far more serious problem, given equal numbers, than the rabbit, and it is possible that it may become a pest of equal importance to the brown rat. Fencing protection, the standby of agriculturists and foresters against most other rodents, is not of the slightest avail against squirrels. It is among agriculturists, especially fruit-growers, that the grey squirrel will cause the greatest consternation, as to them it ranks as a pest of a hitherto unknown kind, while the forester has had ample experience of the destructive powers of squirrels.

There is little doubt that the numbers of grey squirrels will fluctuate periodically as do the numbers of other rodents, when the population has settled down into a state of permanency, and if the fluctuations are as violent as those experienced by the red squirrel it is possible that it will become almost extinct for long periods. In the course of such fluctuations it will be possible to define more accurately the effect which the grey squirrel has upon the numbers of various species of birds, as it would follow that there would be a corresponding fluctuation in the numbers of the birds concerned.

From the opposite point of view it is possible that the grey squirrel may become an important source of revenue as a fur-bearing animal. Though at the present time there is practically no market for this fur, there is no reason why such a state of affairs should continue, for a winter coat of the grey squirrel is of much finer quality than many of the high-priced foreign furs at present in great demand. It is also possible that the flesh of the grey squirrel may become a recognized delicacy, for it is certainly quite palatable if popular prejudice were not against its use for human consumption. The act of placing a commercial price on its head would form a most effective means of keeping down the numbers of the grey squirrel.

Up to the present time no organised control-measures have been adopted, other than shooting in certain areas on the instigation of the owners of estates where they are exceptionally troublesome. But if they become a widespread pest it would be well worth while trying something in the nature of a national squirrel club, on the lines of the Highland Squirrel Club in Scotland. The members of this club pay an annual subscription based on the acreage of woodland on their estates, and the funds thus obtained are used to pay for all the squirrel tails sent in from the estates of the members. By this ingenious system those members who shoot a large number of squirrels actually make a considerable profit over their subscriptions, which gives considerable incentive to keep down the numbers. One member of this club, paying a subscription of £7 5*s*. 0*d*., received £14 2*s*. 0*d*. in tally-money in 1928. As an additional incentive, I believe it is usual for the estate owners to hand over all the profits to their keepers or foresters.

In view of the trouble which is arising from the introduction of the grey squirrel, it would seem advisable to prohibit by law the wilful introduction of alien species without permission from an authority qualified to judge the possible effects of such introductions. Even at the present time new centres are being started by further introductions of grey squirrels into areas as yet unpopulated, though I am informed that the Zoological Society of London refuses to supply squirrels for such purposes.

There is a wide and sadly neglected field for research into such matters as the biological control of animal pests in this country.

13. The Reduction in the Numbers of the Red Squirrel.

There is a widespread impression among people living in the areas colonized by the grey squirrel that the common red squirrel (*Sciurus leucorus* Kerr) has been reduced in numbers or driven out by the introduced aliens. It is quite certain, however, that a remarkable decrease in the numbers of the red squirrel has occurred throughout the whole of Great Britain since the beginning of the present century in all districts alike, both where grey squirrels are present and where none have been seen within a hundred miles.

A good deal of information regarding the fluctuations in numbers of the red squirrel throughout the British Isles has been collected in the course of a parallel investigation to the grey squirrel inquiry, and full details of this will be published later, but a summary is given here of some aspects of this subject which have a bearing upon the ecology of the grey squirrel.

In many instances this decrease in the red squirrel population occurred quite suddenly, the numbers falling from a great abundance to absolute scarcity within the course of one or two years. It has been found difficult to get accurate evidence in all cases regarding the causes of these sudden reductions, but in many instances they are known to have been due to outbreaks of epidemic disease, while in others, for which less complete evidence is available, diseased and dead squirrels were found at the time of the decrease. A few examples of this general decrease are given in tabular form, from different parts of the country, with a summary of the evidence available concerning them. As the position in Ireland is rendered different from that in England, owing to the comparatively recent introductions (or re-introductions) (205) and spread, a separate table is given for cases of decrease occurring in Ireland. Jersey is also included in this table.

From these tables it will be seen that red squirrels have been subjected to a violent reduction in numbers, and that in the majority of instances this could have had no direct connection with the introduction and spread of the grey squirrel. Most of the decreases occurred between 1904 and 1914 in England, but in the mountainous regions of North Wales, Cumberland, and the North of Scotland, the decrease does not appear to have been very marked until about 1920. In many parts of Northern Scotland the numbers were at an extremely high peak about 1907–09, and, though a great reduction did occur immediately after this and on subsequent occasions, red squirrels are far from scarce at the present time in that region.

A complete series of shooting records for the New Forest, Hampshire (formerly Crown Forest, and now Forestry Commission), from 1880 to 1927 is available, and these figures are compiled into a graph of the numbers shot in three-yearly periods (text-fig. 3). I am indebted to the Forestry Commission for permission to use these records. It will be observed that there is a close agreement in the fall in numbers after 1904 on this graph with the observational evidence for the same area given in this table. I may say that the latter information was given to me before the records had been tabulated or examined. (I mention this to show that in this case either the observational evidence or the shooting records could have been used with equal justice as a guide to the date of decrease.) Other features of this curve will be discussed with reference to periodic fluctuations.

14. Disease among Red Squirrels.

From the evidence available I have little doubt that the decrease in numbers since 1900 was mainly due to epidemic disease. The lack of direct evidence of disease in many of the cases of sudden reduction does not in any way prove a negative, as it is extremely difficult to find people at the present time who, if they actually observed such epidemics, have sufficient interest and memory to give the necessary information. On the precise nature of the epidemics among red squirrels very little evidence is forthcoming. The only pathological examinations which I

Table VIII.

Decreases in the Number of Red Squirrels.

District.	Approx. date of decrease.	Disease.	Numbers, 1925–30.	Grey squirrels.	Main source of information.
S.W. Devon	1905	..	Scarce.	None.	211
Mid-Devon	1906–10	..	Scarce.	None.	212
N. Devon	1910–12	Severe.	Scarce.	None.	213
N. Somerset	1914	Severe.	Increase.	None.	214, 215
Dorset	1909–12	Present.	Increase.	None.	216
N. Wilts	1900–11	..	Increase.	None.	87
Savernake Forest	1908–09	Severe.	Scarce.	App. 1925.	91
N. Hants	1905–08	Severe.	..	App. 1927–29.	217217
New Forest	1904–08	Severe.	Increase.	None.	33, 218
Kent	1905–13	Present.	Scarce.	App. 1910–20.	33, 38
N. Oxon	1908–10	..	Scarce.	App. 1913–17.	18, 3
S. Oxon-Berks.	1900–10	Present.	Increase.	App. 1925–28.	130
Epping Forest	1905–10	..	Increase.	None.	177
Bedfordshire	1912	..	Rare.	1890–1920	131
Norfolk	1914–16	..	Increase.	None.	219, 220
Northants	1908–13	..	Scarce.	1910–20	138, 137
Dean Forest	1907–11	..	Increase.	None.	221
Shropshire	1903–10	..	Common	None.	222, 223, 224
N. Staffs	1909–10	Present.	Increase.	None.	225
N. Lincs	1906–09	..	Increase.	None.	217, 226
S. Lincs	1914–16	Present.	Increase.	None.	227, 228
N. and E. Yorks	1906–13	Present.	Local increase	1910–30	170, 153, 152
W. Yorks	1910–14	..	Increase.	1920–30	158
Cumberland	1920–21	..	Increase.	None.	229
N. Northumberland	1910	Present.	Scarce.	None.	233
S. Northumberland	1917–20	..	Increase.	None.	230, 231, 232
S.W. Glamorgan	1913–14	..	Increase.	None.	234
Herefordshire	1913	Present.	..	None.	235
Cardigan	1908	..	..	None.	236
Carnarvon	1914–20	Present.	Increase.	None.	237, 238
N.E. Fife	1906–10	..	..	None.	239
Ross	1910–12	..	Increase.	None.	240
Argyll	1911–12	..	Scarce.	None.	241
Berwickshire	1908–12	Severe.	Increase.	None.	242, 243

Table IX.

Fluctuations of Red Squirrels in Ireland.

District.	First appeared.	Max. period.	Decrease.	Disease.	Numbers, 1928–29.	Source of information.
Wexford	1890	1901–08	1908–09	..	..	244
Belfast	1911	1923–24	1925	Severe.	Scarce.	245, 246
Armagh	1908	1918–24	1924	..	Increase.	247
Londonderry	1899	1924–29	..	..	Numerous.	248
Kilkenny	..	1895–1905	1906–10	..	Scarce.	249
Mullingar	1891	1911–12	1913	..	Scarce.	250
Limerick	1909	1920	1921	..	Scarce.	251
Cork	..	1905–13	1914	Severe.	..	Anon.
Wicklow	1883	1905	1910–14	Severe.	..	252, 205
Louth	1890	1913	1914	..	..	253
Jersey, Channel Islands	1885	1914–25	1925–29	..	Decreasing.	254

Red Squirrels shot in the New Forest, 1880–1927.

Year.	No.	Year.	No.	Year.	No.
1880.. ...	167	1896.....	430	1912.....	140
1881.....	177	1897.....	546	1913.....	208
1882.....	368	1898.....	630	1914.....	283
1883.....	347	1899.....	494	1915.....	275
1884.....	718	1900.....	541	1916.....	213
1885.....	466	1901.....	871	1917.....	196
1886.....	724	1902.. ...	453	19.8.....	45
1887.....	1436	1903.....	895	1919.....	151
1888.....	826	1904.....	412	1920... ..	162
1889.....	2281	1905.....	249	1921.....	176
1890.....	789	1906.....	222	1922.....	100
1891.....	451	1907.....	201	1923.....	111
1892.....	805	1908.....	90	1924.....	131
1893.....	1730	1909.....	116	1925.....	83
1894.....	757	1910.....	116	1926.....	73
1895.....	549	1911.....	111	1927.....	35
				Total ...	21352

have been able to trace are those which were instigated by Mr. Meade-Waldo and carried out by the Pathologist to the London Zoological Society. Examinations of several dead squirrels from Edenbridge, Kent, at intervals between 1904 and 1926, all showed the presence of coccidiosis, and this is presumed to have been the main cause of the decrease in that area (33). It is possible, of course, that all the instances of disease recorded may have been coccidiosis, which is a very common disease among most rodents, but the descriptions of external symptoms from other areas do not entirely agree with this view. For the purposes of this paper, however, it is sufficient to say that many outbreaks of disease of an unknown nature occurred, and were the cause of great mortality among squirrels.

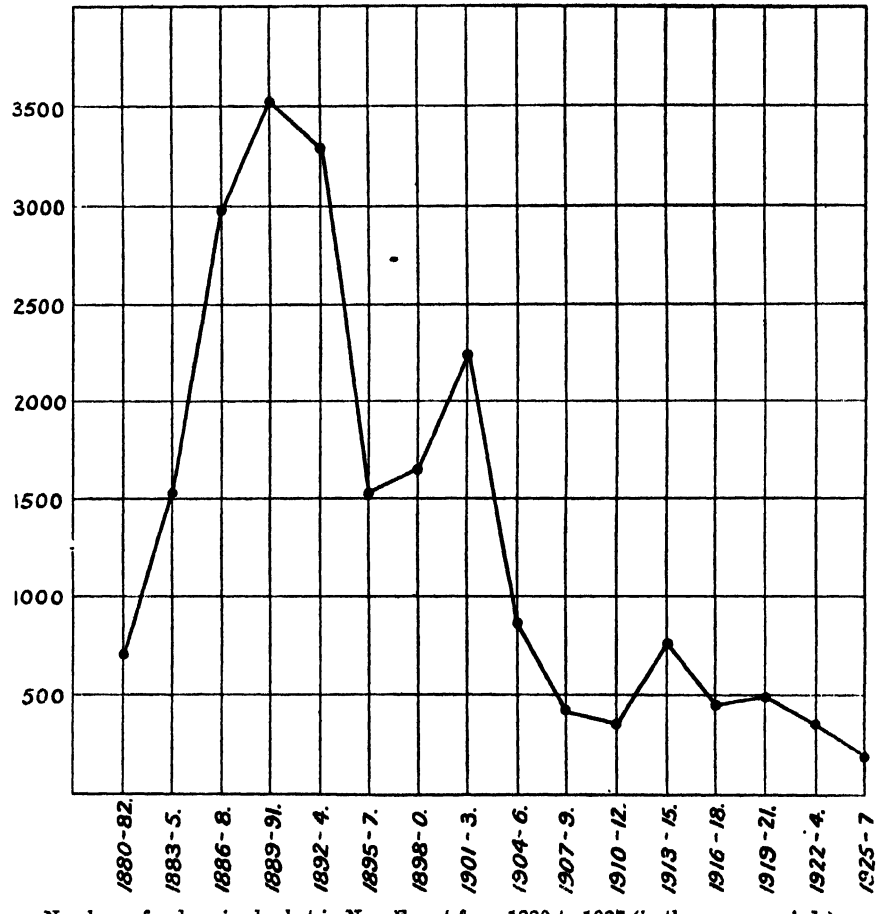
It is possible that the grey squirrel may act as a carrier of a disease which is fatal to the red squirrel but non-pathogenic to the grey species, and the occurrence of so many epidemics after the first appearance of the grey squirrel lends force to this view. But if the introduction of disease occurred with the grey squirrel, one would expect to find indications of epidemics among the red species spreading outwards from the points of introduction of the grey. There is no indication of this, as some of the earliest decreases occurred in the south-west of England, and among the later ones come Norfolk and Lincolnshire—both comparatively near to the Woburn centre of the grey squirrel. Indications of disease were recorded in Inverness-shire in 1862 (206) and there is no reason to believe that such widespread reductions among the red squirrels have not been equally as common in the distant past as during the last thirty years.

15. Fluctuations in the Red Squirrel Population.

The past history of the red squirrel in England is very obscure as regards periods of notable abundance or scarcity, but there is some evidence to show that the numbers have fluctuated considerably over long periods. I have been unable to obtain any evidence which would indicate that red squirrels were ever as numerous during the first half of the 19th century as they became from 1890 onwards. The records from the New Forest show that a period of comparative scarcity must have prevailed immediately prior to 1880, as the squirrels were not

troublesome enough to necessitate shooting before that date, and the records from 1880 show a steady rise to a high peak in numbers about 1890 (see text-fig. 3). This peak was followed by a sharp drop, but another period of abundance was reached in 1901–03, after which the more pronounced decrease followed (corresponding with the epidemic already mentioned), but there is some indication of a further peak in 1913–15. It will be seen that the intervals between these peaks are about twelve years in each case.

Text-figure 3.



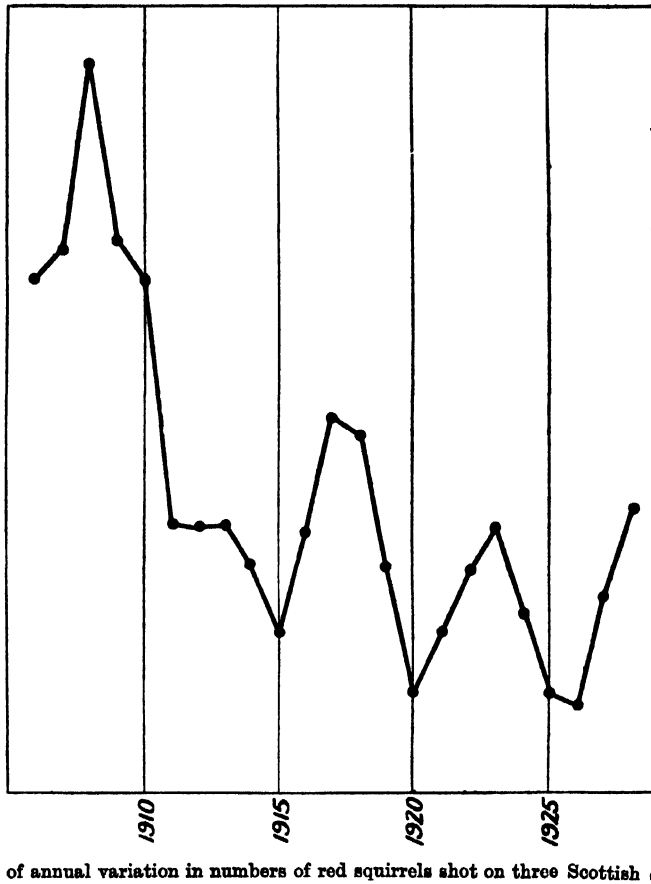
Numbers of red squirrels shot in New Forest from 1880 to 1927 (in three-year periods).

It is interesting to note here that in the woods south-west of Oxford squirrels were noticed to be very numerous about 1876–91, followed by a scarcity. A continuous series of observations from the same area has not yet been obtained, but they were again very numerous in the district in 1907, followed, of course, by the same decrease as experienced in other parts of the country (100).

In Scotland also similar fluctuations have occurred over a considerable period, the periods of greatest abundance being about 1890–1910. In text-fig. 4 the shooting records from three Scottish estates have been combined into a graph of

the numbers shot annually since 1905; it will be seen that similar periodic fluctuations occur in this curve as in that from the New Forest figures, although the peaks do not strictly correspond. The figures on which this graph is based are given below, and form part of the records of the Highland Squirrel Club, to the Secretary of which I am indebted for allowing me to use them (207). The Highland Squirrel Club was started in 1903, in an attempt to combat the serious damage to forestry caused by the depredations of red squirrels. The three estates

Text-figure 4.



Graph of annual variation in numbers of red squirrels shot on three Scottish estates. (Smoothed A + B + C.)

from which the figures for this graph are obtained were chosen as those likely to have the most constant area of woodland and the most uniform shooting activity throughout the period. The complete record of the Highland Squirrel Club cannot be used to show natural fluctuations, as the number of members has not been constant throughout the whole period of its activity; it may be mentioned, however, that a total of over 82,000 squirrels has been accounted for from 1903 to 1929, and the activities of the club are confined to about 36 estates in the north of Scotland.

Red Squirrels killed on three Scottish Estates, 1905–29.

Year.	Beaufort.	Ardross.	Novar.	Total.
1905.....	671	144	107	922
1906.....	913	236	134	1283
1907.....	1428	443	364	2235
1908.....	762	80	254	1096
1909..	1314	906	97	2317
1910.....	768	267	205	1240
1911.....	668	138	76	882
1912.....	657	167	90	914
1913.....	612	482	137	1231
1914.....	583	188	123	894
1915.....	429	189	70	688
1916.....	576	109	150	835
1917.....	734	562	184	1480
1918.....	859	286	206	1351
1919.....	474	134	114	722
1920.....	523	147	37	707
1921.....	417	207	28	652
1922.....	631	319	126	1076
1923.....	686	287	64	1037
1924.....	608	240	77	925
1925.....	362	156	52	570
1926.....	497	30	49	576
1927.....	557	280	24	861
1928.....	846	262	93	1201
1929.....	711	215	157	1083

Table X.

Localities in England and Wales where Red Squirrels have shown an Increase in Numbers in the Period, 1925–30.

Locality.	Source of information.	Locality.	Source of information.
Street, Somerset	214	N. Lincs	217, 227
Wimborne, Dorset	255	Wharfedale, Yorks	158
Blandford, Dorset	256	Goathland, Yorks	153
Swindon, Wilts	87	Skelmanthorpe, Yorks	264
Calne, Wilts	257	Ribston, Yorks	177
Wickham, Hants	258	Coniston, Lancs	265
New Forest, Hants	218	Lake district, Cumberland–Westmorland..	108, 229
Churt, Surrey	259	Whittingham, Northumberland .	232
Haslemere, Sussex	260	Radnorshire	266
Hambledon, Surrey	72	S.W. Glamorgan	234
Wyfold Court, Oxon	130	Anglesey	268
Epping Forest, Essex	177	Portmadoc, N. Wales	269
Downham, Norfolk	220	S. Denbighshire	270
Merton, Norfolk	261	Carnarvon district	237
Tenbury, Worcester	262		
Coleford, Gloster	263		

In Table X. a number of districts are given where a noticeable increase in the numbers of red squirrels has taken place during the period 1925–30. All these localities, with the exception of Hambledon, Surrey, where grey squirrels appeared in 1928, are free from grey squirrels at the present time. In no district where the grey squirrel has become established is any revival in the numbers of the red

species recorded up to date, but it will be seen that the slight increase during the past few years has not become general in all the areas where no grey squirrels are present, so that it is probably only the very beginning of a general increase of the red squirrels.

From the evidence available there seems little doubt that the red squirrel population has always been subject to marked fluctuations in numbers, and, though at present the periodicity of these fluctuations does not appear to be regular in all localities, it is probable that when more continuous and accurate data are available it will be found that there is a natural cycle in the numbers, as is known to be the case with many other rodents (202, 203, 208, 209).

16. The Inter-relations of Red and Grey Squirrels.

In view of the fluctuations in the red squirrel population, and the fact that the increase of the grey squirrel coincided with a period of natural depression among the native species, it is impossible at the present time to make any definite assertions regarding the effects of the introduced aliens on the red squirrels in this country. As there have been indications during the last few years of a revival in the numbers of the red squirrel, it is probable that another period of abundance is approaching, and in that event there will be plenty of evidence available regarding the relations between the two species.

Several instances of actual fights between the two species, resulting in victory for the grey, have been reported, but several cases have also been found of red and grey squirrels living amicably together in the same district, so that the evidence either for or against any active animosity between the two is at present quite inconclusive. It may be mentioned that in America the red squirrel is invariably the more pugnacious of the two, and has repeatedly been seen chasing and attacking the larger grey squirrel, much to the discomfiture of the latter (210). It may be well to mention here the fallacious but frequently repeated story which has arisen in America that the red squirrels castrate the greys by biting off their testes (210). A reversal of this story has been adopted in this country, where it is often stated that the grey squirrel castrates the red. In the British Isles, so far as I am aware, there is not a shred of evidence to support such a theory, and in America it was based upon a few solitary cases of apparent castration. The testes of most squirrels, in common with other rodents, are extremely small during the winter months so that the external scrotum is very inconspicuous in the winter as compared with the summer breeding condition; consequently it is very easy, by superficial observation, to mistake this winter condition for castration.

Whereas the red squirrel in its favourite haunt, the conifer forest, has a very limited food-range, consisting of seeds, bark, buds, and fungi, the grey squirrel is not specialized in this manner, and favours a much wider range of food-stuffs. It has already been stated, when discussing the habitat of the grey squirrel, that an opportunity of observing whether it will live in pure coniferous areas in this country has not yet arisen, so that it is impossible to say whether the future will show a clearly-marked division between the red squirrel habitat in the coniferous woods and that of the grey squirrel in the mixed deciduous woods and more open areas. But the existence of this well-defined distinction in America makes it appear unlikely that the grey squirrel will ever adapt itself to the specialized life in the pine-forests of the Scottish Highlands, and it is probable that the large coniferous forests recently planted throughout Great Britain will form strongholds of the red squirrel, immune from serious competition with the grey species. There is bound to be competition, and perhaps antagonism, on the border-zones of these habitats, and it is possible that the red squirrel will be severely restricted in choice of habitat by the grey squirrel, but it is also possible that the latter will be driven away from the habitats most favoured by the native species.

The third possibility, though hardly a likely one, is that the two species will live together in all habitats quite amicably. But whatever may be the future relations of the two, there is no evidence at the moment on which to base the supposition that the red squirrel will inevitably be exterminated by the grey. A sudden decrease in the numbers of the grey which may occur in the future, in the course of a natural periodicity in numbers, will perhaps be wrongly attributed to the attacks of the red squirrels.

17. Summary.

In this paper details are given of 33 centres of introduction of grey squirrels (*Sciurus carolinensis*) in the British Isles during the period 1889–1930, and it is shown that grey squirrels were present in this country in some places as early as 1828. By 1930 the grey squirrel had populated a total area of approximately 13,350 square miles, mainly in Southern England, Cheshire, and Yorkshire, and there is every reason to believe that it will eventually cover the whole country with the possible exception of mountainous districts such as Northern Scotland.

The British red squirrel (*Sciurus leucorous*) is subject to pronounced fluctuations in numbers, and a great decrease occurred about 1904–14 throughout the whole country, being apparently due to disease. There is some evidence of a revival of the red squirrel population during the past few years. The decrease of red squirrels appears to have no connection with the spread of the grey squirrel, and little evidence is yet available regarding competition or antagonism between the two species.

18. References.

Correspondents and Persons interviewed.

Ref. No.	Name.	Ref. No.	Name.
1.	Mr. E. Simpson.	41.	Mrs. Winshurst.
2.	Mr. R. E. Knowles.	43.	Mr. G. A. White.
4.	Mr. E. M. Harting.	44.	Mr. G. L. Villier.
5.	The Duke of Bedford.	45.	Miss V. E. Buxton.
6.	Dr. E. St. Lawrence Finny.	46.	Miss C. L. Read.
7.	Mr. W. H. Benden.	47.	Mr. H. E. Littledale.
8.	Sir P. Chalmers Mitchell.	48.	Mr. T. Hendrie.
9.	Mr. W. H. St. Quintin.	49.	Mr. N. S. Lucas.
10.	Viscount Astor.	50.	Mr. J. H. Newman.
11.	Mr. Guy Nickalls.	51.	Col. J. S. O. R.-Luxford.
12.	Mr. J. Reed.	52.	Mr. E. Aston.
14.	Mr. J. Small.	53.	Mr. H. W. Stone.
15.	Lord Granard.	55.	Mr. C. E. Shipley.
16.	Mr. H. C. Hunt.	56.	Mr. E. Bartlett.
17.	Mr. R. Fortune.	57.	Mr. F. Faraker.
18.	Mr. G. Tickner.	58.	Mrs. G. G. Miller.
19.	Mrs. L. Cooke.	59.	Mr. M. Burr.
20.	Mr. J. W. Lee.	60.	Mr. A. T. Townsend.
23.	Mr. W. Felsted.	61.	Mr. C. J. Davies.
24.	Mr. W. Greaves.	62.	Mr. P. Hanson.
25.	Mr. Wilkinson.	63.	Mr. A. Boarder.
31.	Mrs. F. M. Adeney.	64.	Mr. D. B. Oram.
32.	Mrs. Sandford.	65.	Mr. J. Sweet.
33.	Mr. E. G. B. Meade-Waldo.	66.	Mr. G. I. Scott-Moncrieff.
34.	Mr. J. A. Harrison.	67.	Mr. A. S. Juniper.
35.	Mr. A. E. Ralph.	68.	Mr. A. Beadell.
36.	Miss F. Walker.	69.	Mr. E. J. Arcott.
37.	Mr. J. E. Little.	70.	Mr. A. Simpson.
38.	Mr. R. M. Prideaux.	71.	Mr. J. H. S. Burton.
39.	Mr. J. B. Ridgwell.	72.	Mr. E. Parker.
40.	Col. W. F. Blaker.	73.	Mr. S. H. Priestley.

Ref. No.	Name.
74.	Mrs. E. M. Swaine.
75.	Mr. S. Lawrence.
76.	Mr. W. M. Bevan.
77.	Mr. A. M. Coulson.
78.	Mr. R. Butler.
79.	Maj. Sir H. B. Peirse.
80.	Mr. E. C. Cope.
82.	Mr. H. D. Carroll.
83.	Mr. J. B. Colvin.
84.	Mr. A. B. Hornblower.
85.	Marquis of Ailesbury.
86.	Mr. C. E. J. Crawford.
87.	Rev. E. H. Goddard.
88.	Mr. J. Brown.
89.	Major M. Portal.
90.	Lord Selborne.
91.	Mr. W. T. Arnold.
92.	Dr. W. Balgarnie.
95.	Mr. J. Fathur.
96.	Miss K. Conran.
97.	Miss M. Leveson-Gower.
98.	Miss N. D. Stevens.
99.	Mr. T. D. Wynne-Weston.
100.	Mr. W. Payne.
101.	Mr. H. Mathesor.
102.	Dr. L. H. Jackson.
103.	Mr. A. J. C. George.
104.	Mr. H. Barnett.
105.	Col. M. A. C. Crowe.
106.	Rev. S. E. Chavasse.
107.	Mr. R. E. Steavonson.
108.	Mr. C. S. Elton.
109.	Mr. R. Fisher.
110.	Mr. H. Corvin.
111.	Mr. A. E. Price.
112.	Dr. A. H. Foster.
113.	Mrs. M. A. Gates.
114.	Mr. C. Oldham.
115.	Mr. R. W. Hickling.
116.	Mr. H. Lidstone.
117.	Mr. E. N. Lane.
118.	Mr. G. Arnett.
120.	Mr. White Thompson.
121.	Mr. F. B. Pursell.
122.	Mr. R. B. McKerrow.
123.	A. D. Middleton.
124.	Miss E. M. Markland.
125.	Mr. Oliver Watney.
126.	Mr. J. Lamb.
127.	Mr. T. A. Rose.
128.	Countess of Longford.
129.	Rev. J. E. Barles.
130.	Lord Wyfold.
131.	Mrs. E. G. Lindsell.
132.	Mr. M. Godfrey.
133.	Mr. S. W. Leeson.
134.	Mr. W. A. Walker.
135.	Mr. G. H. Gulliver.
136.	Mr. H. B. Hall.
137.	Mr. T. Jones.
138.	Mr. J. R. Middleton.
139.	Mr. G. Bullock.
140.	Mr. T. W. Deane.
141.	Mr. C. Lowe.
142.	Mr. M. Walker.
143.	Mr. R. Campion.
144.	Mr. W. S. Joyce.
145.	Mr. W. N. Lindley.
146.	Mr. A. R. Thompson.
147.	Mrs. M. J. Patteson.
148.	Mr. S. A. Waterson.
149.	Mr. A. P. Pridhume.
150.	Dr. O. H. Wild.
151.	Miss S. Butlin.
152.	Mr. A. Gordon.
153.	Mr. F. J. Flintoff.
154.	Mr. W. Brown.
155.	Miss C. Prestin.
156.	Mr. C. T. Webster.
157.	Mr. C. Julian.
158.	Mr. H. B. Booth.
159.	Mr. F. H. Edmondson.
160.	Mr. H. Hirst.
161.	Mr. J. Green.
162.	Mr. F. H. Ball.
163.	Mr. V. C. Wynne-Edwards.
164.	Mr. R. B. Wilson.
165.	Mr. P. Baldwin.
166.	Mr. P. Smith.
167.	Mr. S. Smith.
168.	Mr. J. England.
169.	Mr. C. R. Busfield.
170.	Mr. W. J. Clarke.
171.	Mr. M. Odling.
172.	Miss J. B. Kitson.
173.	Mr. J. Richardson.
174.	Mr. J. Morris.
175.	Mrs. S. O. Plant.
176.	Mr. J. Hogg.
177.	Mr. G. Dent.
178.	Mr. H. Masterman.
179.	Mr. E. W. Wade.
180.	Dr. W. Baigent.
181.	Mr. T. A. Coward.
182.	Mr. W. R. Dalzell.
183.	Mr. T. Wilson.
184.	Mr. R. S. Brown.
186.	Dr. H. M. Steven.
187.	Mr. W. D. Russell.
188.	Rev. T. V. Morley.
189.	Mr. J. Gunn.
190.	Mr. H. J. Howard.
191.	Mr. H. P. Jones.
195.	Mr. J. A. Sweetlove.
197.	Mr. H. S. Illingworth.
199.	Mr. F. J. Cox.
200.	Mr. W. James.
201.	Rev. Canon A. T. Barnet.
207.	Mr. A. H. Duncan.
211.	Mr. W. A. Evans.
213.	Mr. C. S. Saxton.
214.	Mr. H. Underwood.
215.	Col. Pretor-Pinny.
216.	Mrs. E. M. Degad.
217.	Mr. W. Tribe.
218.	Mr. L. S. Osmaston.
219.	Mr. G. Gurney.
220.	Mr. R. Stocks.
221.	Mr. A. H. Popert.
222.	Mr. G. Potts.

Ref. No.	Name.
223.	Mr. H. E. Forrest.
224.	Miss Frances Pitt.
225.	Mr. J. R. B. Masefield.
226.	Sir G. Whichcote.
227.	Mr. T. C. P. Beasley.
228.	Capt. J. Reeve.
229.	Mr. A. Astley.
230.	Mr. F. W. Hall.
231.	Mr. R. Douglas.
232.	Mr. W. J. Bewick.
233.	Mr. G. Elliott.
234.	Mr. R. Cory.
235.	Mr. G. E. Blundell.
236.	Mr. H. M. Vaughan.
237.	Major O. Greaves.
238.	Mr. J. R. Davies.
239.	Mr. W. Berry.
240.	Mr. G. G. Johnstone.
241.	Mr. Kennedy.
242.	The Earl of Home.
243.	Mr. R. Johnston.
244.	Mr. C. B. Moffat.
245.	Mr. T. Byers.
246.	Mr. J. A. S. Stendall.

Ref. No.	Name.
247.	Mr. J. R. O. Cope.
248.	Miss L. MacCulloch.
249.	Mr. G. L. Murray.
250.	Rev. P. Poe.
251.	The Knight of Glin.
252.	Mr. C. Ball-Acton.
253.	Mr. G. H. Pentland.
254.	Mr. G. F. B. de Gruchy.
255.	Miss K. A. Ricardo.
256.	Mr. W. Ford.
257.	Mr. A. O. Hood.
258.	Capt. A. Arnold.
259.	Mr. C. G. O. Bond.
260.	Mr. E. M. Nicholson.
261.	Mr. F. Woolsey.
262.	Rev. A. Ellison.
263.	Mr. W. J. Humphries.
264.	Mr. F. Lawton.
265.	Mr. W. G. Wilson.
266.	Mr. P. Harrison.
268.	Miss S. F. Lloyd.
269.	Mr. M. Speake.
270.	Mr. F. C. Best.
271.	Miss M. Halkett.

Literature References.

3. Boyd Watt, H. On the American Grey Squirrel in the British Isles. Essex Naturalist, vol. xx. pp. 189–205, 1923.
13. Theobald, F. V. The American Grey Squirrel in Kent, Sussex, and Surrey. Bulletin of S.E. Agric. College, March 1926.
21. Ritchie, J. Scottish Naturalist, 1923, pp. 93–4.
22. ——— Animal Life in Scotland, pp. 288–290, 1920.
26. "C. F. S." Yorkshire Weekly Post, Jan. 19th, 1929, p. 24.
27. Francklyn, P. Country Life, April 6th, 1929.
28. The Cambrian Quarterly Mag. & Celtic Repertory, vol. ii. p. 351, 1830.
29. Pratt, H. S. Vertebrate Animals of U.S.A. Philadelphia, 1923.
30. Harrison, W. H. Daily News, Feb. 3rd, 1930.
42. Hill, H. The Gamekeeper, Jan. 1930.
54. The Gamekeeper, Jan. 1930.
93. Bagnall, R. D. The Gamekeeper, Dec. 1929.
94. "B. E. S." The Field, April 24th, 1918, p. 566.
119. Frost, T. R. The Gamekeeper, Dec. 1929.
158. The Glasgow Naturalist, vol. v. p. 40, 1913.
192. Seton, E. T. Journ. of Mammalogy, vol. i.
194. Twist. The Gamekeeper, Jan. 1930.
196. The Gamekeeper, Feb. 1930.
198. Baldwin, W. H. Journ. of Mammalogy, vol. viii. p. 57, 1927.
202. Middleton, A. D. Cycles in the Numbers of British Voles (*Microtus*). Journ. of Ecology, vol. xviii. pp. 156–165, 1930.
203. Elton, C. S. Plague and the Regulation of Numbers in Wild Mammals. Journ. of Hygiene, vol. xxiv. p. 2, 1925.
204. Philips, C. Trans. New Zealand Inst. 1890, pp. 319–325.
205. Barrington, R. M. On the Introduction of the Squirrel into Ireland. Proc. Royal Dublin Soc. 1880.
208. Elton, C. S. The Relation of Animal Numbers to Climate. Proc. Conf. of Empire Meteorologists. London, 1929.
209. ——— Animal Ecology. London, 1929.
210. Hatt, R. T. The Red Squirrel. Roosevelt Wild Life Annals, vol. ii. no. 1. 1929.

EXPLANATION OF THE PLATES.

PLATE I.

MAP 1.—Introduction of grey squirrels into the British Isles, 1889–1930.
(The numbers refer to list in Table I.)

PLATE II.

MAP 2.—General distribution of grey squirrels in the British Isles in 1930, with main centres marked.

PLATE III.

MAP 3.—Distribution of grey squirrels by 1930 in S.E. England and Midlands.

PLATE IV.

MAP 4.—Distribution of grey squirrels in Yorkshire by 1930.

PLATE V.

MAP 5.—Distribution of grey squirrels in the Cheshire district and North Wales by 1930.

PLATE VI.

American Grey Squirrel (*Sciurus carolinense*).
British Red Squirrel (*S. leucorous*).

EXHIBITIONS AND NOTICES.

May 6th, 1930.

Prof. E. W. MacBride, M.A., F.R.S., Vice-President, in the Chair.

The Secretary communicated the following note he had received on two Lion-Tiger Hybrids now in the collection of the Munich Zoological Gardens:—

"Visitors to Munich's Zoo in Hellabrun can now see two hybrids from a lion as sire and a tiger as dam. They are now a year and three-quarters old and are developing splendidly. The two—both are females—vary from both sire and dam in the shape of the skull and their colouring. Instead of the sharp profile of the lion's head and the curve of the tiger's skull, both these hybrids have gently sloping profiles. Their colouring is darker than that of the lion, and the tiger's characteristic stripes, although present, are a reddish brown instead of black. Both animals are comparatively tame.

"The sire of the Munich hybrids, who is also in the same Zoo, is an especially beautiful and well-developed specimen of the North African Atlas lion, which is somewhat smaller than the East African lion, but much more graceful and comely. This species is gradually dying out, and there are probably few zoological gardens anywhere that possess as fine a specimen as "Sultan" of Munich, with his magnificent black neck and the long mane along the median line of the lower side of the body—a special characteristic of the Atlas lion. The dam is a Sumatra tiger which was bred in the zoological garden at Frankfort-on-Main. These so-called island tigers are small compared with the royal tiger, but with more strongly marked striping."

Miss E. M. Brown, B.Sc., exhibited, and made remarks upon, some Protozoan Parasites of Fishes.

Mr. E. G. Boulenger, F.Z.S., exhibited, (1) living specimens of the Poison-Frog (*Dendrobates tinctorius*), and (2) a male specimen of the Midwife-Toad (*Alytes obstetricans*) carrying the eggs.

May 20th, 1930.

The Lord Rothschild, D.Sc., Ph.D., F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of April 1930:—

The registered additions to the Society's Menagerie during the month of April were 620 in number. Of these 45 were acquired by presentation, 546 were purchased, 11 were deposited, 2 were received in exchange, and 16 were born in the Menagerie.

The following may be specially mentioned:—

2 Lion Cubs (*Felis leo*), from Kenya, presented by Dr. Martinellia on April 15th.

6 Blackbuck (*Antilope cervicapra*), from India, presented by H.H. The Maharaja of Jaipur on April 22nd.

1 Rheinard's Pheasant (*Rheinardia ocellata*), from Annam, presented by Mons. J. Delacour, F.Z.S., on April 9th.

Major S. S. Flower, O.B.E., F.Z.S., exhibited, and made remarks upon, a series of photographs of Gorilla, Elephant Seals, and other animals now living in the Carl Hagenbeck Tierpark at Stellingen, near Hamburg.

Mr. D. Seth-Smith, F.Z.S., exhibited three lantern-slides from photographs he had taken of a young Pigmy Hippopotamus (*Chæropsis liberiensis*) and made the following remarks:—

The female Pigmy Hippopotamus presented to the Society by the New York Zoological Society as a Centenary gift gave birth to a calf on May 11th at 8.30 A.M. in her den, the period of gestation having been 247 days.

The pond was at once cleaned and refilled, and at 4 P.M., when the temperature of the water had been raised to about 90° Fahr., the door leading from the den to the pond was opened. The Hippo., however, showed no inclination to go into the water but stayed with her calf in her den for the rest of the day. At times she lay on her side with her back facing us so that it was impossible to see if she was suckling the calf.

Head-Keeper Bowman stayed in the house all the first night. At 11 P.M., when I left, mother and calf were fast asleep, but at 11.30 the mother turned over on her side and suckled the calf for some twenty minutes. This was repeated at 2 A.M. and at 4.30 A.M. At 5.30 A.M. the mother went into the bath, leaving her calf asleep in the den. Here she stayed for nearly an hour, then went back to the calf, which she suckled every two hours. It was not until 6 P.M. on Sunday, 34 hours after the birth, that the mother and calf went into the water together. The latter swam well and seemed quite at home, and from then the mother suckled it under the water about every two hours. They were still in the water at 8 A.M. the next morning, shortly after which they both returned to the den and went to sleep, and the two remained sleeping until 3 P.M.

These habits differ somewhat from those of *Hippopotamus amphibius*, which takes its calf to the water immediately after birth and apparently never suckles it on land.

The Pigmy calf appeared to be about sixteen inches in length at birth, and was able to walk well from the first.

It was timed to remain under the water for periods of some thirty seconds.

The mother, while mostly suckling the calf when in the water, was noticed occasionally to do so on land, sometimes when standing, the calf going down on its "knees" like a young pig.

Col. A. E. Hamerton, C.M.G., D.S.O., F.Z.S., exhibited a collection of photographs illustrating his "Remarks on Trypanosomiasis in relation to Man and Beast in Africa."

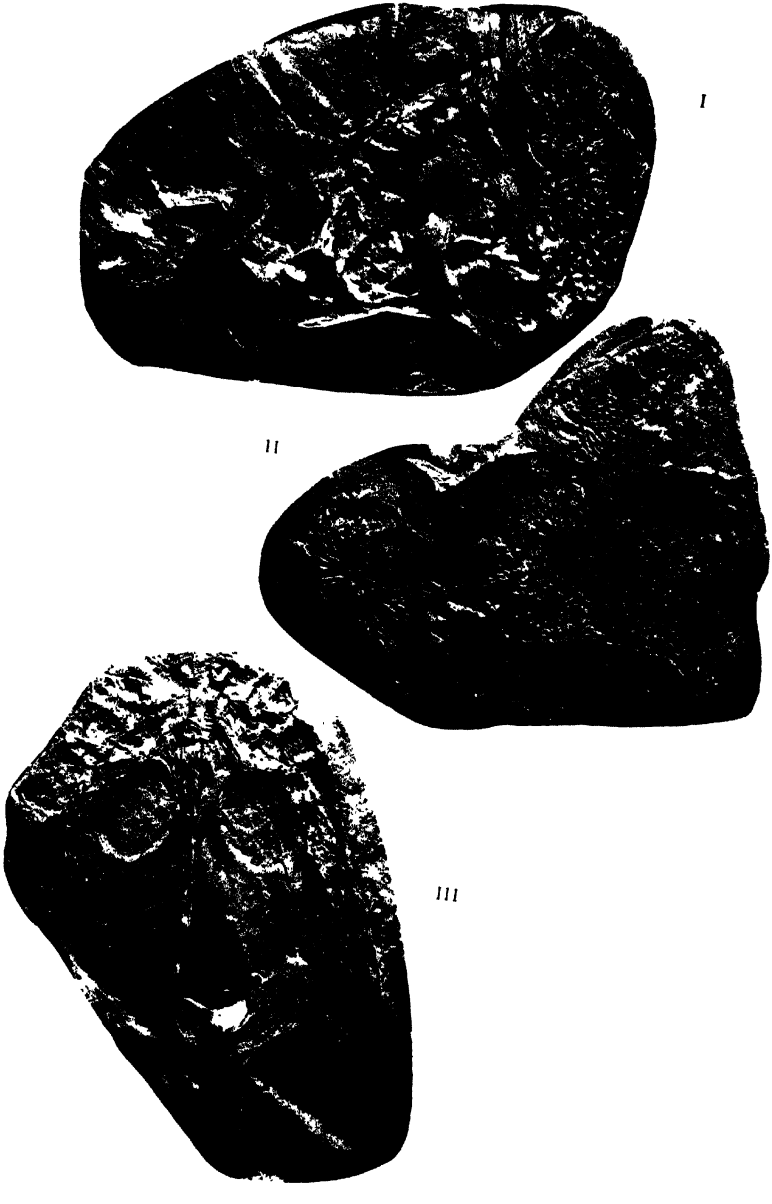
June 3rd, 1930.

Sir ARTHUR SMITH WOODWARD, F.R.S., Vice-President, in the Chair.

Mr. J. R. NORMAN, F.Z.S., exhibited, and made remarks upon, the Pectoral Fin of an exceptionally large Flying-Fish (*Exocœtus fernandezianus*) from Juan Fernandez collected by Mr. Arthur Haserick, F.Z.S.

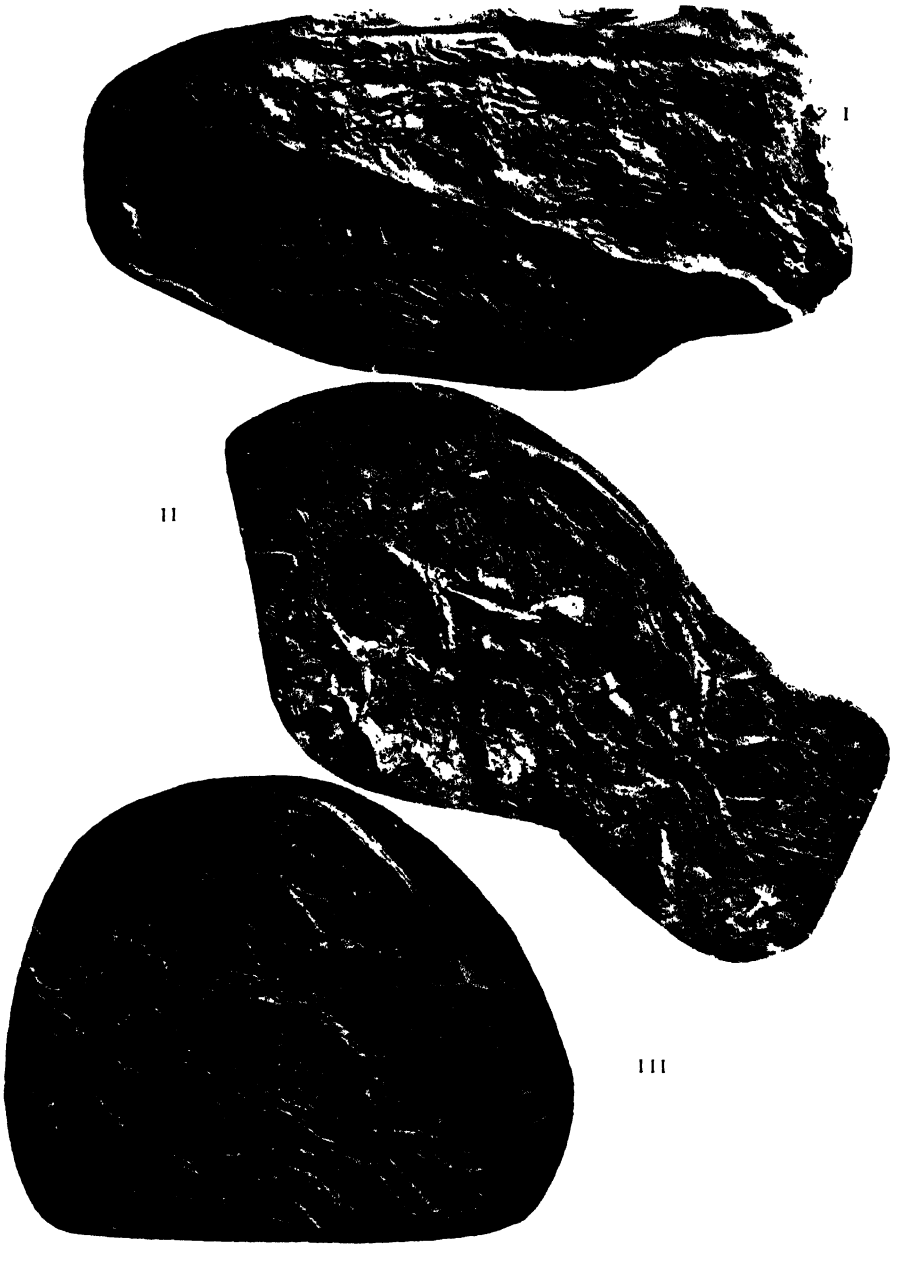
Col. S. MONCKTON COPEMAN, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a rare variety of the Waved Umber Moth, *Hemerophila abruptaria* var. *unicolor*, caught on Primrose Hill.

[Proceedings, 1930, Part II. (pp. 261–548), was published on August 14th, 1930.]



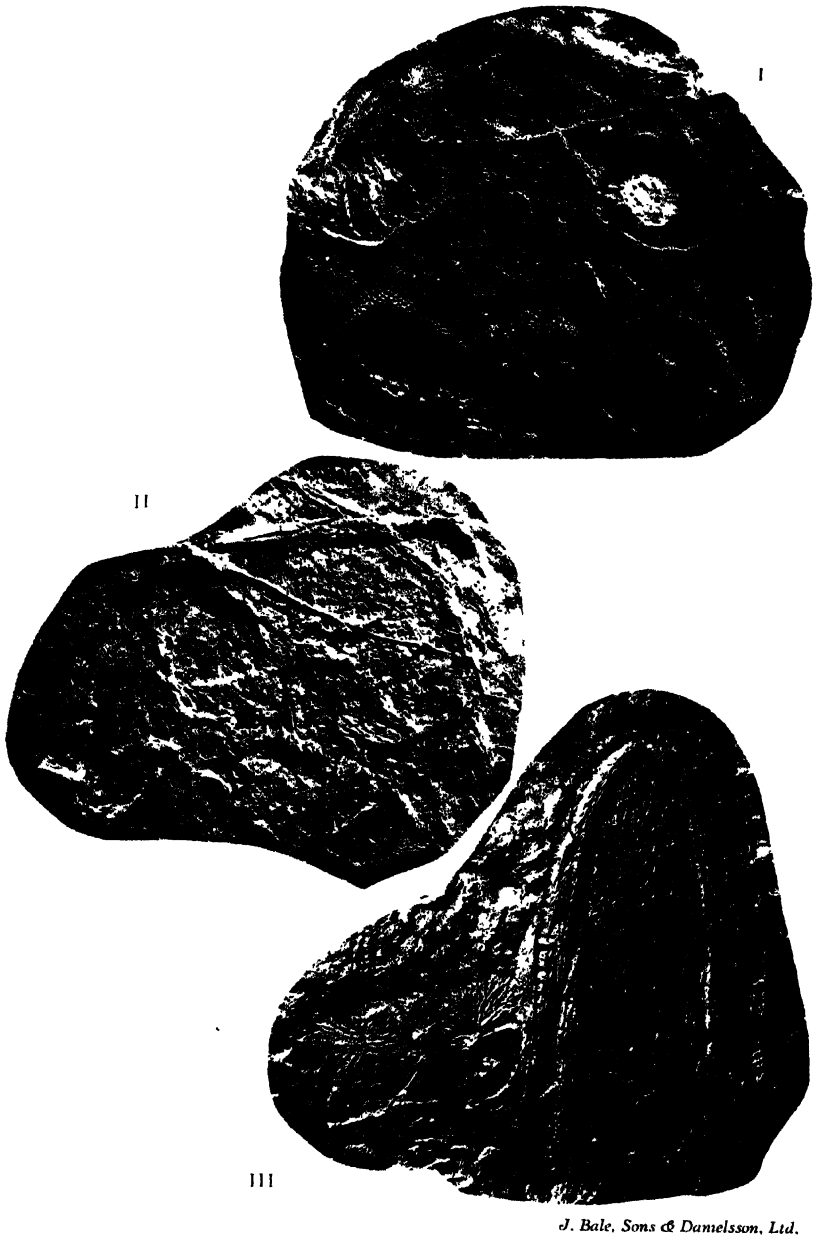
J. Bale, Sons & Danielsson, Ltd.

ERPETOSAURUS RADIATUS AND E. LAEVIS.



J. Bale, Sons & Danielsson, Ltd.

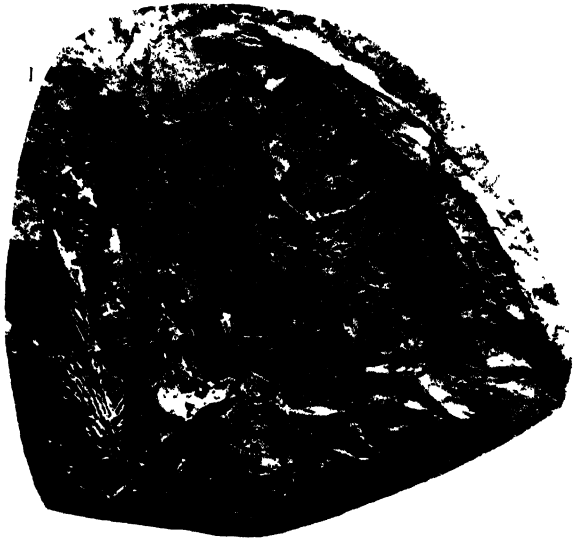
COLOSTEUS SCUTELLATUS AND *STEGOPS DIVARICATA.*



J. Bale, Sons & Danielsson, Ltd.

PLATYRHINOPS MORDAX AND *MYTARAS MACROGNATHUS.*

I



II



J. Bale, Sons & Danielsson, Ltd

PELION LYELLI AND *PHYLLOSPONDYLIAN VERTEBRAE.*

I



II

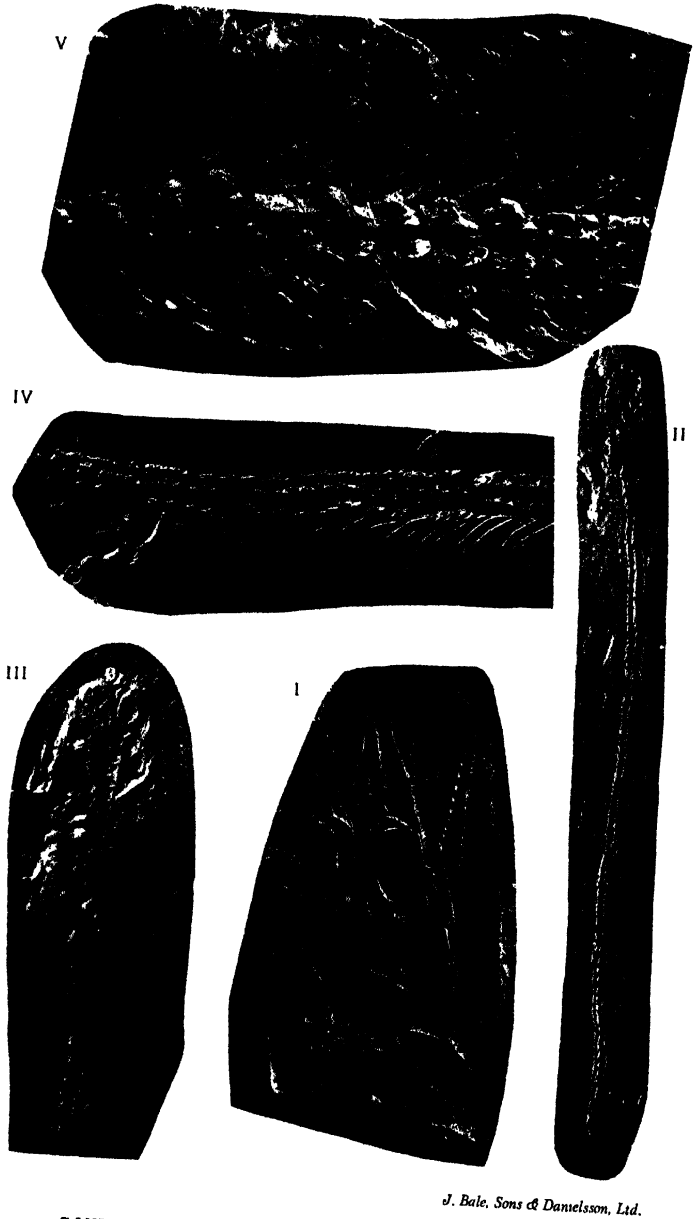


III



J. Bale, Sons & Danielsson, Ltd

OPHIDERPETON AMPHIUMINUS.



J. Bale, Sons & Danielsson, Ltd.

SAUROPLEURA MARSHII, COCYTINUS GYRINOIDES AND *PLEUROPTYX CLAVATUS.*

39. The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio.

By MARGARET C. STEEN, B.Sc. (Zoology Department, University College, London.)

[Received May 6, 1930: Read June 3, 1930.]

(Plates I.–VI.*; Text-figures 1–21.)

CONTENTS.

	Page
Introduction	849
Method of Preparation	850
Drawing and Reconstruction	851
Classification	851
Order PHYLLOSPONDYLI	852
Erpetosaurus radiatus (Cope)	852
Erpetosaurus lævis (Moodie)	856
Colosteus scutellatus (Newberry)	858
Stegops divaricata (Cope)	860
Platyrhinops mordax (Cope) (gen. nov.)	865
Mytaras macrognathus (gen. et sp. nov.)	868
Pelion lyelli Wyman	869
Order LEPOSPONDYLI	874
Ophiderpeton amphiuminus (Cope)	874
Sauropleura marshii (Cope)	877
Sauropleura pectinata (Cope)	877
Order ADELOSPONDYLI	881
Cocytinus gyrinoides Cope	882
Pleuroptyx clavatus Cope	885
Order LABYRINTHODONTIA	886
Orthosaurus sp.	886
Labyrinthodont	886
The Structure of the Vertebral Column in the Phyllospondyli	886
The Linton Phyllospondyli	887
Geographical Distribution	889
List of Works cited	889
Explanation of the Plates	890
Abbreviations used in the Text-figures	891

INTRODUCTION.

Fossil remains of Amphibia from the Coal Measures of the world are extremely rare, and are known only from a few restricted localities in America and Europe. One of the chief American localities is that of Linton, Ohio, and it is with the British Museum collection of Linton Amphibia that this paper is concerned.

Amphibian material from Linton was first described by Newberry in 1875, and later by Cope, who figured and described a large number of genera and species. The fauna was finally monographed by Moodie in 1916. Extremely little, however, has been known of the structure of the animals which compose it, and their classification is unsatisfactory.

At Professor D. M. S. Watson's suggestion, I examined the British Museum collection of Amphibia from the Middle Coal Measures of Linton, Ohio. This collection, made over fifty years ago, was in the possession of J. W. Davies, and reached the Museum after his death. It has remained untouched since that time. The material when received showed little or no structure, but after preparation such excellent results were obtained that it is now possible to form some real idea of the morphology of the animals represented in the collection and of their relationships.

It was impossible for me to identify the bulk of the material as the type-specimens were inaccessible, and the literature inadequate for this purpose. Professor A. S. Romer, of Chicago, who published this year an excellent paper on the American collections of Linton material, recently visited University College and examined the British Museum collection; to his kindness I owe the identification of most specimens. It is, moreover, satisfactory that our results are generally in agreement.

I wish to take this opportunity of thanking Professor D. M. S. Watson, F.R.S., in whose department this work was carried out, not only for the great interest he has taken and the generous help he has given me, but also for the original inspiration to examine this material.

Some of the photographs, from which the text-figures used here were made, were taken by Mr. J. Thomas, of the Zoological Dept., University College, to whom I wish to express my thanks.

Finally, I wish to thank the Department of Scientific and Industrial Research for the grant which has enabled me to undertake this work.

Method of Preparation.

The source of the Linton material is a thin band of cannel coal, found in association with true coal. All evidence as to the formation of these bands suggests that they represent muds containing organic detritus, laid down in extensive pools or shallow lakes, which lay isolated amongst the vast Carboniferous forests.

The British Museum collection consists of thirty-seven specimens, and contains some exceptionally good skulls. Three specimens show almost the entire animal, seventeen of the remaining specimens are skulls, of which two are fragmentary; with some, body remains are associated. The rest of the material consists of fragments of vertebral column, vertebræ and ribs, body scaling, one interclavicle, and one lower jaw. Although small, this collection contains specimens of most species present in the fauna of the Linton cannel coal bed.

The skulls of Amphibia from Linton have hitherto shown no structure since they appear as a dull fractured face when found, but on treatment with hydrochloric acid the bone dissolves completely away, leaving on the cannel coal a clear and distinct impression. Small specimens were put face downwards in a shallow bath of acid, while the larger specimens were surrounded by a plasticene wall, inside which an acid pool could be formed. The object is to have as little as possible of the matrix in contact with the acid. No definite concentration of acid was used, since concentrated hydrochloric acid added directly to the pool of water gave the best results. In many of the specimens the bone seems to be preserved partly as pyrite, and where this is so the action is much slower. After exposure to acid for some time, the surface of the specimen degenerates into a black spongy mess on which the acid has no further effect. This condition was avoided by frequently removing the specimen and brushing under the tap with a stiff brush, so that a fresh surface is exposed. The time taken in the preparation of a specimen varies from two to ten days. In some cases prolonged soaking in water is necessary

to ensure complete removal of the calcium chloride formed during preparation before the specimen will dry quickly *.

The skulls are usually dorsoventrally flattened, indicating that the heads in life were broad and flat. This compression has in some specimens brought the ventral surface of the skull roof into contact with the dorsal surface of the palate, so that both the ventral surface of the palate and the inner surface of the skull roof are often superimposed on the same impression. The perfection of the preservation facilitates the interpretation of such specimens.

Drawing and Reconstruction.

The following method was employed to ensure accuracy in drawing. The actual specimen was taken, and all details of structure (sutures, lateral line, etc.) outlined by painting with Chinese white under a binocular microscope. These were photographed. The photographs were lined in with Indian ink, and the sutures checked from a plasticene squeeze observed under a binocular microscope. From these inked photographs tracings were taken and line drawings made to correspond with the squeezes (*i. e.*, laterally reversed). The existing plates and figures being so inadequate it was thought worth while to include photographs of squeezes of almost all the specimens and labelled line drawings to form keys to them.

The reconstructed drawings were made from these tracings. Both dorsal surface and palate may be shown by the squeezes, either in a single specimen, or where both slab and counterpart have been preserved. In such cases it is possible to draw reconstructions of the skull with considerable accuracy. The appearance of all the specimens suggests that the palate was flat. Crushing therefore, although it may have displaced bones, will not have altered their width to any appreciable extent. If, then, tracings of the palatal bones be replaced so that they articulate accurately, a complete palate will be reformed, and so the relative positions of the tooth-bearing margins of the premaxillæ and maxillæ fixed. If the quadrate is present, or if its width can be ascertained in any way, the position of the quadratojugal can be established, thus completing the outline of the skull.

The dorsal surface is then restored on the assumption that the interorbital region and the table which lies behind it are flat. The positions which the sutures of the other bones of the skull will occupy on dorsal projection are determined by noting the widths of the individual bones along a transverse line on a strip of paper. The strip is then bent, so that the margins of the skull are the correct distances apart, as determined by the palatal reconstruction, and the section appears reasonable.

In the reconstructions of the dorsal surface of the skulls any asymmetry which is shown on the specimen has been retained. The palates have all been made symmetrical by a compromise between the actual outlines of the bones of each side, as they were symmetrical during life.

A few specimens were outlined by painting sutures, etc., with Chinese white and drawn directly by means of a camera lucida.

Classification.

The classification of the Palæozoic Amphibia is based primarily on structural differences in the vertebral column. Four types of vertebræ, between which no intermediate morphological forms are known, are present throughout their evolutionary history. These types are distinguished easily from one another in fossil material, and thus, although their morphological nature is uncertain, provide a sound basis for classification.

* Durofix, manufactured by the Rawlplug Co. Ltd., was found to be an excellent preparation for all repairs. It is a cellulose nitrate product, soluble in amyl acetate, is unaffected by hot or cold water, and unattacked by hydrochloric acid. Where reinforcement was necessary dental stone was used.

The morphology of the Labyrinthodontia is now well known, so that the classification of this group rests on satisfactory evidence. The much smaller animals included in the Lepospondyli, Adelospondyli, and Phyllospondyli are, with the exception of the genera of the typical Branchiosaurs and a few isolated species, very incompletely known. Hence the existing classifications are valueless.

The Linton fauna (with the exception of the Adelospondyli and two specimens of Labyrinthodontia) falls into two distinct groups. One, the Lepospondyli includes animals with a well ossified and massive vertebral column always very easily seen. The other group includes a series of related forms with no apparent vertebral column in association with the skulls. These, on the evidence afforded by the character of the skull, the structure of the palate, and the incomplete ossification of the vertebral column, belong to the Phyllospondyli. The complete evidence for their position in this group and a discussion of the significance of their structure in a consideration of the evolution of the Phyllospondyli occur later in this paper.

Order PHYLLOSPONDYLI.

Genus ERPETOSAURUS Moodie, 1909.

Moodie, 1909, Bull. Amer. Mus. Nat. Hist. xxvi. p. 348.
Moodie, 1909, Proc. U.S. Nat. Mus. xxxvii. p. 21.

The genus *Erpetosaurus* is represented in the British Museum collection by two skulls which differ in details of palatal structure and clearly represent two distinct species. One skull, of which the dorsal surface of the skull and the palate are present, is identical in the ornament of the cranial bones with *Erpetosaurus radiatus*. In the second specimen only the palate and the inner surface of the cranial roof are known. This skull is identical with Romer's figures of the type of *Diceratosaurus lævis*. It is proposed to call this second species *Erpetosaurus lævis*.

ERPETOSAURUS RADIATUS (Cope).

Cope, 1874, Trans. Amer. Phil. Soc. xv. p. 273, fig. 10.

Material:—

R. 2670. Impression of the posterior half of the palate and of the occiput (Pl. I. fig. 1; text-fig. 1).

P. 2672. Impression of the external surface of the skull and of the shoulder-girdle, counterpart slab to R. 2670 (Pl. I. fig. 2; text-figs. 1 & 2).

Interclavicle, humerus, cleithrum, and ilium found in association with R. 2670, P. 2672 (text-fig. 3).

R. 2660. Specimen showing ventral scales, interclavicle, and vertebral elements.

Measurements:—

Length of orbit, 13 mm.; breadth of orbit, 11 mm.; interorbital distance, 6·5 mm.; breadth of table and skull, 32 mm.

The skull of *Erpetosaurus radiatus* is represented by two impressions of the same individual skull, one of the palate and the other of the dorsal surface of the skull. It is the only specimen in the entire collection to retain the occiput.

In the impression on the palate (Pl. I. fig. 1), of which the posterior half only is preserved, the bones remain practically *in situ*, except for the slight displacement due to dorso-ventral crushing. The parasphenoid is small with its posterior limit well marked, laterally its suture with the basisphenoid is not determinable. The processus cultriformis runs forward as a stout rod, convex ventrally, for some distance, but it is incomplete anteriorly. The basipterygoid processes are small and well formed, and have a movable articulation with the pterygoids. There is no trace of carotid foramina.

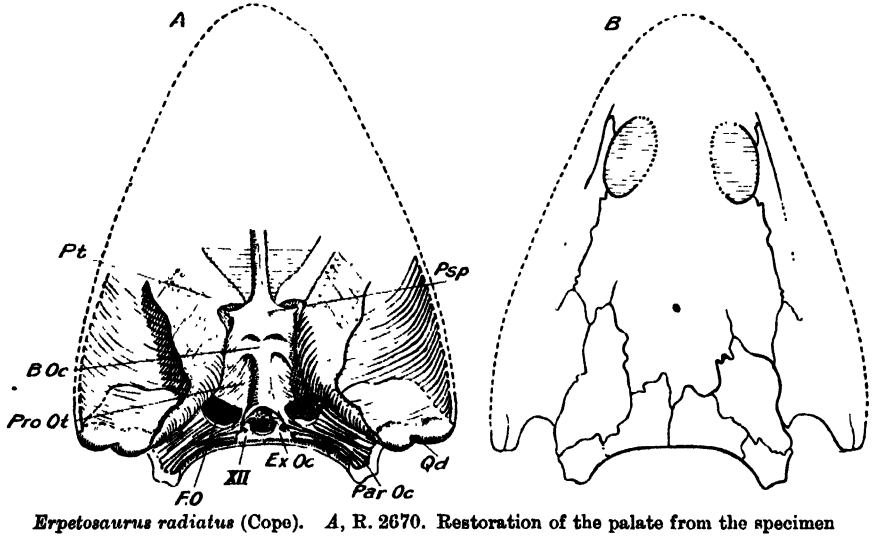
Posterior to the parasphenoid the basis cranii is completed by the basioccipital

bone. The ventral surface bears a strong keel which separates two depressed areas for the insertion of the recti capitis muscles. The posterior or occipital face of the basioccipital forms the oval condyle, which is deeply concave; the exoccipitals are small, they form the lateral margins of the foramen magnum, and enter into the condyle. On the lateral surface at the suture with the opisthotic there is a notch present which represents the foramen for the vagus nerve. There is also a small foramen present in the exoccipital bone for the transmission of the XIIth nerve.

The otic bones of the right side only are preserved. The paroccipital process is stout and runs out laterally and dorsally towards the tabular region of the skull. The fenestra ovalis is very large, its smooth margin is formed anteriorly by the prootic, posteriorly by the opisthotic. Through this fenestra a smooth sheet of bone is seen which represents the roof of the saccular cavity, and above which lies the bone in which the semicircular canals are housed.

The interpterygoid vacuities are small compared with those of the other

Text-figure 1.



Erpetosaurus radiatus (Cope). *A*, R. 2670. Restoration of the palate from the specimen figured, Pl. I. fig. 1. *B*, P. 2672. Dorsal aspect of the skull. ×1·33.

Phyllospondylian species in this fauna. The pterygoids are massive bones, the palatal ramus is broad and practically flat, and the margin of the pterygoid which bounds the interpterygoid vacuities is smooth and slopes gently to this broad shelf. Both palatal and quadrate rami are covered with close-set tubercles or little teeth. Very perfect facets for articulation with the basipterygoid processes of the parasphenoid transversely truncate the upturned smooth margins of the pterygoids. The quadrate ramus runs back in an almost vertical position to the quadrate. Here the quadrates are ossified so that the palatal width is known and the outline of the skull can thus be restored.

The presence of one small plate on the parasphenoid suggests the former presence of palatal ossifications such as Romer found in one of his specimens.

The dorsal surface of the skull is represented by an impression of the external surface of the right half of the skull roof (Pl. I. fig. 2). All the sutures are certain, but there is a bad break across the squamosal which was at first troublesome. The posterior margin of the table of the skull is deeply concave, and from

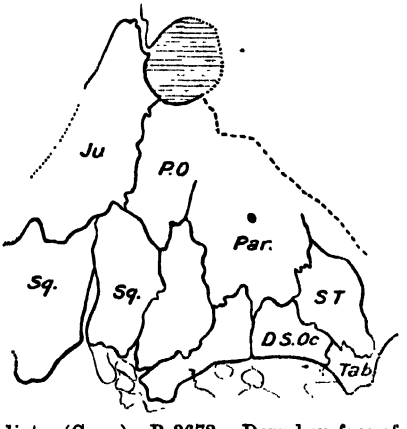
the dermo-supraoccipitals and tabulars thin flanges extend on to the occipital surface.

The parietals together form a large bone on which no median suture is visible, and whose shape is characteristic. There is a pineal foramen; anterior to this the skull roof is not preserved. The tabulars are small, their free margins forming blunt square-shaped corners to the table of the skull. The supra-temporal is extremely broad.

The side of the skull is incomplete, but the outline of the orbit is preserved ventrally by the presence of both jugal and lachrymal and dorsally by an elevation on the matrix. The orbits are situated very far forward, and the interorbital width is small. No supraorbital or sclerotic plates are present, jugal and post-orbital are incomplete, and the squamosal is unusally deep.

When restored the skull is high. The occiput is deep and slopes forward steeply towards the palate. It is not possible to check the accuracy of the restoration by the height of the occiput, as there is no indication where the flanges, which extend

Text-figure 2.



Erpetosaurus radiatus (Cope.) P. 2672. Dorsal surface of the skull figured in Pl. I. fig. 2. ×0·95.

from the dermo-supraoccipitals and tabulars on to the occipital surface of the skull, come into contact with the paroccipital process, etc.

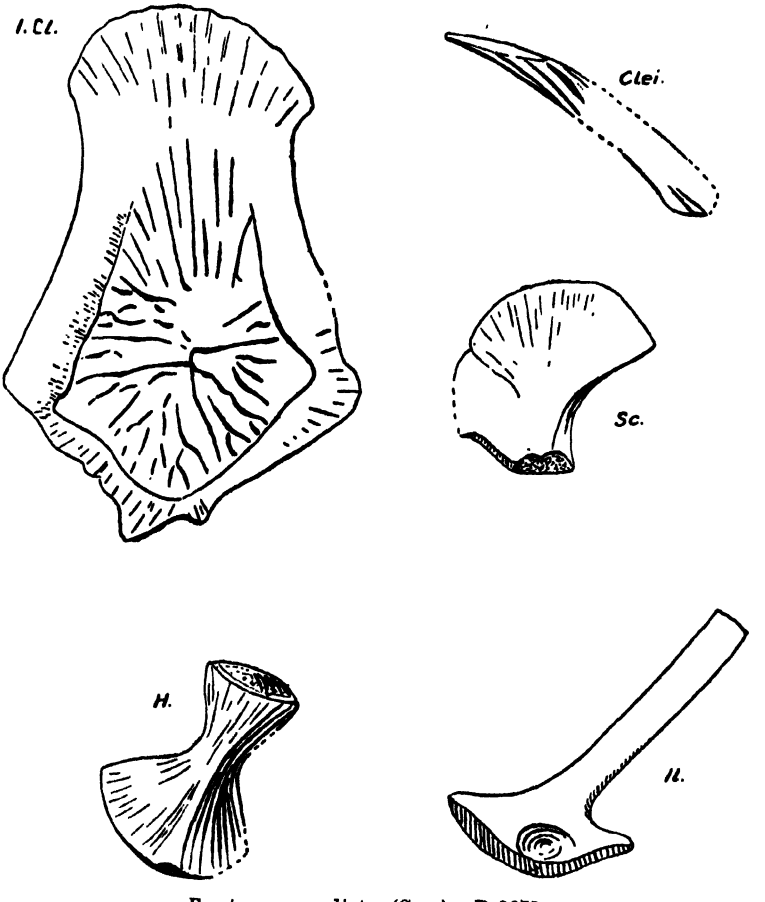
The ornament, which is characteristic of the species, is shown on Pl. I. fig. 2. No lateral line canals are present.

The palate of *Erpetosaurus radiatus* is important as a morphological stage in the evolution of the Amphibian skull. It is extremely primitive in many respects. The interpterygoid vacuities are narrower than in the other Phyllospondylian species of this fauna, the parasphenoid small and quite unlike the broad plate-like structure of the later Branchiosaurs, and the basioccipital is large. The articulation between the parasphenoid and the pterygoids is movable. Further, the large basioccipital condyle is a pit, and the exoccipital contributions to the single condyle small. The palate therefore forms a morphological stage equivalent to that of Eryops among the Labyrinthodontia.

In association with the skull of *Erpetosaurus radiatus*, various isolated limb bones, vertebral elements, and scales are preserved. The interclavicle is massive and bears a coarse reticulate ornament resembling that of the skull. This ornament stops short at the inner edge of the overlapped margins. In the scapula the ventral end and the posterior margin are thickened while the blade is thin. The

humerus is small and presents an expanded and rounded head, from which the bone contracts to a slender shaft; the distal end is also expanded—this expansion is flat. The ilium is the only pelvic girdle bone known in the collection, and is Amphibian in structure. The dorsal process is long and slender, and the expanded ventral end shows two facets for the articulation of the pubis and ischium; the acetabulum is shallow with a distinct rim.

Text-figure 3.



Erpetosaurus radiatus (Cope). P. 2672.
I.Cl., Interclavicle, × 1·84; *Il.*, Ilium, × 2; *Sc.*, Scapula, × 2; *Cl.*, Cleithrum, × 2
R. 2670. *H.*, Humerus, × 1·6.

The vertebral elements are flat somewhat triangular plates (in height 10 mm. and 5 mm. long), with a roughened surface, the reverse side on the counterpart slab being smooth. Similar elements occur in association with the skull of *Stegops divaricata* (R. 2546), and in the specimen R. 2644 on which the body-remains of a Phyllospondyl are preserved (Pl. IV.). Scales of two types are also associated with the skull of *Erpetosaurus radiatus*; the ventral scales are large (3 mm. by 7 mm.),

smooth on both inner and outer sides, parallel-sided with rounded ends, one end being slightly narrower than the other. Smaller fragile oval dorsal scales are also present which show a delicate concentric and radial ornament. The specimen R. 2660 exhibits identical ventral scales, and vertebral elements in association with an interclavicle (of the same type as that of *Erpetosaurus radiatus*) and ribs (in length 12 mm.) which are short, straight, and expanded at both ends. Here the vertebral column consists of a more or less complete single row of plates continued from the interclavicular region for some 12 mm. posteriorly; the structure of the plates through this length of column is uniform, but posteriorly they decrease in size (height 10–6 mm.). No dorsal scales appear to be preserved in this specimen.

ERPETOSAURUS LÆVIS (Moodie).

Moodie, 1909, Journ. Geol. xvii. no. 1, p. 63, figs. 13, 14.

Material:—

R. 2662. Impression of the palate on which the sutures of the inner surface of the skull roof are also visible (Pl. I. fig. 3; text-figs. 4 & 5).

Measurements:—

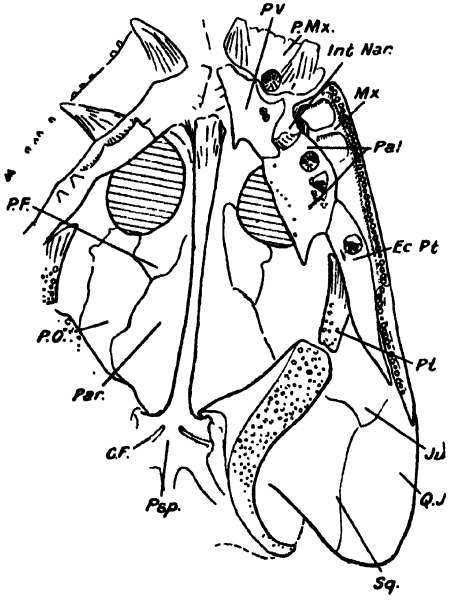
Length of orbit, 10 mm.; breadth of orbit 8 mm.; interorbital width, 5 mm.

One of the most complete palates in the collection is that of *Erpetosaurus lævis*. Compression during fossilization has slightly displaced the individual bones, and the pterygoid is fractured.

The parasphenoid consists of a narrow processus cultriformis and a widened posterior plate. The basipterygoid processes are small and face rather anteriorly. Two foramina, through which the internal carotid arteries enter the skull, are present on the parasphenoid, and from each of these the groove for the artery runs outwards to the margin of the bone. Posterior to the parasphenoid two deep grooves enclose between them a convex medial ridge. These grooves mark the insertion on the basioccipital of the recti capitis muscles (which arise from the cervical vertebræ). The condyle is not present. The processus cultriformis is expanded at the anterior end, and shows on either side grooved articulating facets for the prevomers.

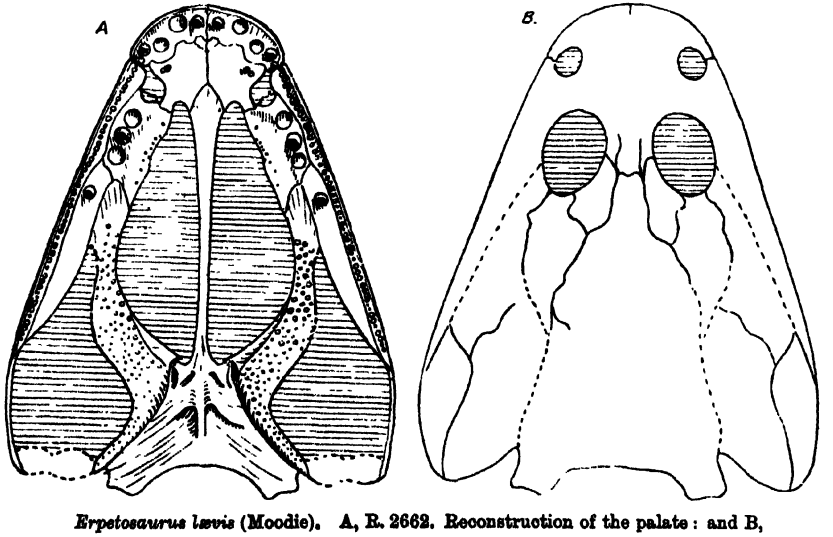
The ptergyoids are massive trifid bones. The palatal ramus is flat. The margin of the pterygoid which bounds the interpterygoid vacuity is smooth and slopes dorsally to this broad flat ramus. Except for this smooth sloping margin, the surface of the pterygoid is heavily tuberculated. Very smooth facets for articulation with the basipterygoid processes of the parasphenoid transversely truncate this smooth anterior face. The interpterygoid vacuities are elongate, and the margin is completed anteriorly by the palatines and prevomers. The palatines are wide and their palatal surface is stepped, so that the part of the bone adjoining the maxilla is more ventral than the flat flange bounding the interpterygoid vacuity. This marginal flange is thin, and several small tubercles occur near its inner margin. The palatine enters into the margin of the internal nares and extends dorsally as a concave bony flange to form in part a posterior roof to the internal nares. Into the margin of the nares the prevomer, premaxilla, and maxilla also enter. The prevomers meet one another in the mid line. The premaxillæ are short and have a marginal ridge bounding a steeply concave surface on which the large premaxillary teeth are inserted. Two large teeth with their replacement pits are present and a single small posterior tooth. The maxilla extends on the palatal surface as a thin strip to the level of the basipterygoid processes; it is displaced, so that the flange which extends over the palatine is visible. Here a marginal ridge is also present, on the inner side of which lies a continuous series of teeth and pits. These teeth are numerous, small, and decrease slightly in size posteriorly. Wedged in between the pterygoid and maxilla and posterior to the

Text-figure 4.



Erpetosaurus lævis (Moodie). R. 2622. Drawing of the specimen figured in Pl. I. fig. 3. × 1·54.

Text-figure 5.



***Erpetosaurus lævis* (Moodie). A, R. 2662. Reconstruction of the palate: and B, dorsal aspect of the skull. × 1·34.**

palatine lies the ectopterygoid. Between this bone and the pterygoid there is an extension of the subtemporal fossa anteriorly (*cf.* Branchiosaurus). That this is so is also evident in the specimen figured by Romer. The lateral portion of the palatine bears a large tooth and two pits for replacing teeth, the prevomer has a small tooth and a pit for its fellow, and the transverse bone a single large tooth. The larger teeth show longitudinal striation towards their bases. No supraorbital or sclerotic plates are present. Part of the inner surface of the roof of the skull is visible through the interpterygoid and subtemporal vacuities (text-fig. 4). The resemblance to *Erpetosaurus radiatus* where the sutures are shown on the external surface of the skull is exact. Although closely allied to *Erpetosaurus radiatus* this form is placed in a separate species. The nature of the specimen limits the specific characteristics, but the specific distinction is based on the following:—

Different skull proportions, *e.g.* less elongate basioccipital, narrower smooth upturned face of pterygoid, narrower otic notch; and the presence of carotid foramina on the parasphenoid.

Genus Colosteus Cope, 1875.

Cope, 1875, Geol. Surv. Ohio, p. 405.

Colosteus scutellatus (Newberry).

Newberry, 1856, Proc. Acad. Nat. Sci. Philad. xviii. p. 98 (*Pygopterus scutellatus*).

Cope, 1869, Trans. Amer. Philos. Soc. p. 22, pl. 36, figs. 1, 2 (*Colosteus scutellatus*).

Material:—

R. 2547. Impression of the external surface of the complete left half of skull and of the anterior part of both lower jaws (Pl. 11. fig. 1; text-figs. 6 & 7).

Measurements:—

Interorbital distance, 20 mm.; breadth of table of skull, 54 mm.

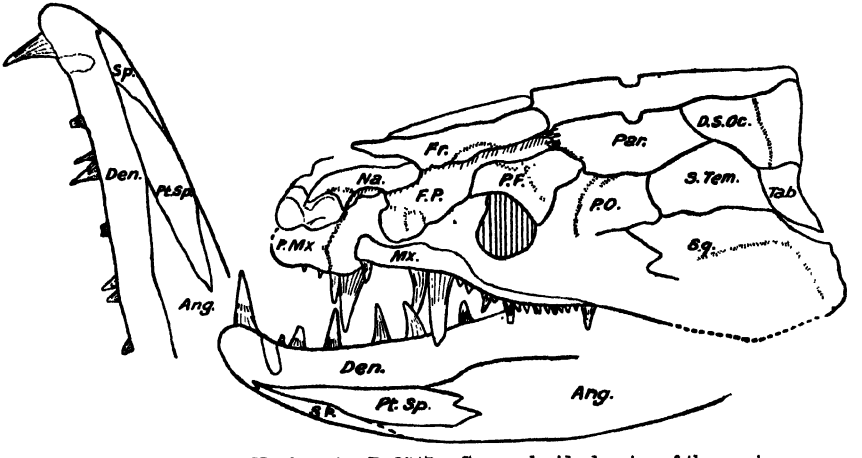
The skulls of *Colosteus scutellatus* as shown in fossil material are usually crushed sideways so that a lateral impression of the skull is preserved. This type of preservation is unique amongst Amphibian skulls, and indicates, as Romer has pointed out, a high arched skull.

This specimen, R. 2547, is the counterpart of the type-specimen of *Sauropleura longidentata* Moodie (No. 8619 G. Mus. Nat. Hist.). No body-remains are associated with the skull, except for a fragmentary shoulder-girdle.

There is no evidence of the external nares since the anterior part of the skull is imperfectly preserved. The orbits are situated in the anterior half of the skull length, but the interorbital distance is greater than in *Erpetosaurus radiatus*. The structure of the skull is shown in text-figs. 6 & 7. The parietals are broad and enclose a large pineal foramen; the anterior surface shows a groove articulating face for the frontal. The frontal is long, narrow, pointed anteriorly, and has been displaced. Anterior to the frontal lies a nasal bone. The sutures between jugal, postorbital, and squamosal are in part visible. It is interesting that the postorbital reaches to the parietal as in *Erpetosaurus*. The supratemporals are large, broad, and stretch from the postorbital to the tabulars. On this specimen the tabular clearly projects somewhat backwards, ending in a narrow point.

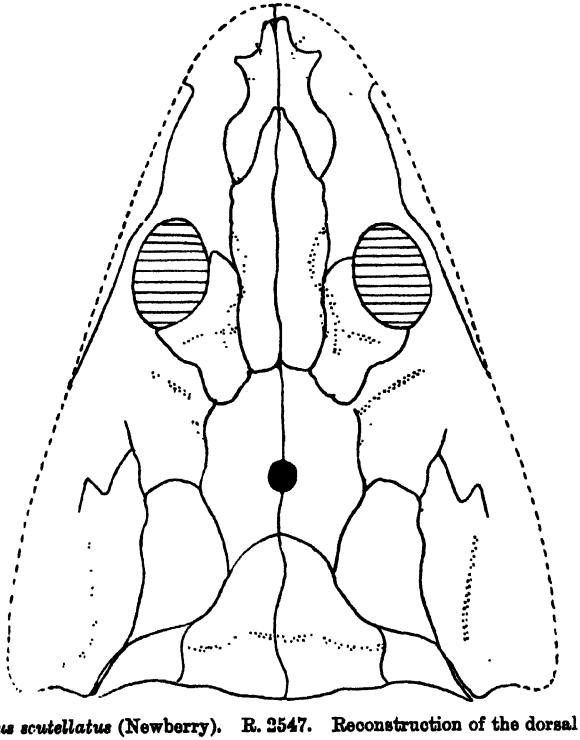
The lower edge of the cheek posterior to the maxilla is preserved on the slab as a depression. The jugal forms part of the free ventral margin of the cheek. The premaxilla and maxilla are both shown, and bear along their edges a series of small teeth. Besides these marginal teeth, several large palatal teeth are present. Both palatal and marginal teeth, as well as those present on the lower jaw, show a very characteristic longitudinal striation of the dentine.

Text-figure 6.



Colosteus scutellatus (Newberry). R. 2547. Camera lucida drawing of the specimen figured in Pl. II. fig. 1. × 0·74.

Text-figure 7.



Colosteus scutellatus (Newberry). R. 2547. Reconstruction of the dorsal aspect of the skull. × 1·06.

The condition of the lateral line is interesting and agrees with the condition which Romer found in his specimens. The occipital commissure runs as a deep groove across the dermo-supraoccipitals. It stops abruptly at the margin, and there is no trace of lateral line canal on the tabular bone. The supraorbital canal stretches from the frontal on to the post-frontal, and there forks. There is a lateral line groove across the post-orbital and on the squamosal and premaxilla The groove on the premaxilla runs to the extreme ventral edge of the bone. This condition is known in only one other Amphibian, the Embolomerous form *Orthosaurus*. It is interesting that the condition should now be paralleled in a Phyllospondylous form. There appears to be no lateral line groove on the lower jaw in this specimen.

The external surface of both lower jaws is shown. The dentary is large and forms the greater part of the anterior ramus of the jaw. A series of large pointed teeth are carried by the dentary which are extremely characteristic both in their arrangement and in the longitudinal striation of their dentine. The anterior tooth is the largest, and behind this, on each jaw, and on the external surface of the dentary, there is a definite groove for the accommodation of the large prevomer tooth. The lower jaw teeth in this specimen form one series and do not appear to be spaced in relation to the palatal teeth; they are therefore dentary and not coronoid teeth. The splenials wrap round the ventral anterior edge of the jaw and appear on the external surface as narrow splints; posterior to this postsplenials are present. The anterior ramus is certainly slenderer than in the restoration of the lower jaw as figured by Romer. The evidence afforded by this specimen is in agreement with Romer's conclusion that *Colosteus* is a Phyllospondyl. There is nothing in the structure of the skull which precludes the relationship, and in form and structures this skull resembles that of the other Phyllospondylian species.

That the vertebræ and ribs known as Molgophis and Pleuroptyx can be assigned to this form is highly improbable. In some of the American specimens, body remains of *Colosteus* occur in association with the skull, but Romer states that there are no "describable remains of vertebræ" present. The Pleuroptyx vertebræ are massive, with well-developed neural arches, and heavily ossified centra. This is not the type of vertebra which could be associated with a Phyllospondylian skull, or which would be imperfectly preserved. Further, the lengths of Pleuroptyx vertebræ preserved indicate a long-bodied animal, a form unusual amongst Phyllospondyli. It is probable that *Pleuroptyx clavatus* can be more satisfactorily assigned to the order Adelospondyli, for reasons which will be pointed out when the structure of the vertebral column of this species is considered (see p. 885–6).

Genus Stegops Moodie, 1909.

Moodie, 1909, Journ. Geol. xvii. p. 79.

Stegops divaricata (Cope).

Cope, 1885, Proc. Am. Phil. Soc. xxii. p. 406 (*Keraterpeton divaricatum*).

Material:—

R. 2668. Impression of the external surface of the skull and of the right lower jaw (Pl. II. fig. 3; also text-figs. 8 & 10).

R. 2546. Impression of the ventral surface of the palate, one lower jaw in position. Inner surface of skull roof visible through the interpterygoid vacuities and posterior to the parasphenoid. Remains of fore limbs, shoulder-girdle, scales, neural arches, and vertebral elements present (Pl. II. fig. 2; also text-figs. 9 & 10).

P. 2671. Impression of palate, very imperfect.

Measurements:—

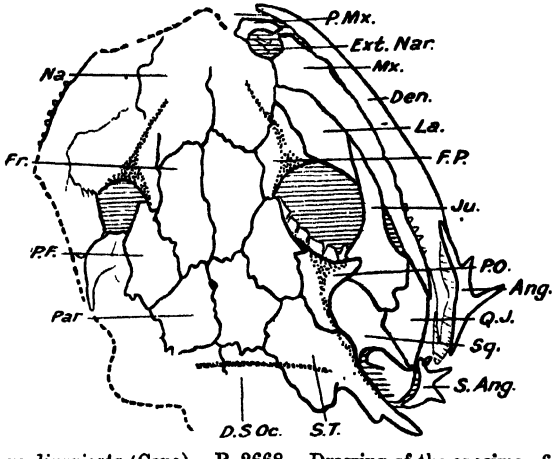
	R. 2546.	R. 2668.
Length of orbit	13 mm.	11 mm.
Breadth of orbit	11 mm.	10 mm.
Interorbital distance	16 mm.	16 mm.
Breadth of table of skull	22 mm.	—
Length of skull in median line	46 mm.	—
Length of lower jaw preserved	—	55 mm.

The two specimens of *Stegops divaricata*, R.2668, R.2546, between them give the complete structure of the skull.

An impression of the dorsal surface of the skull is retained in R.2668 (Pl. II. fig. 3). All the sutures are certain. The posterior part of the table of the skull is incomplete, as the tabulars are wanting and only the anterior margins of the dermo-supraoccipitals are present.

The parietals are smaller than the frontals or nasals, and enclose a small pineal foramen near their anterior margin. A further peculiarity of this species is the extremely large supratemporal bone continued posteriorly as a free spine,

Text-figure 8.



Stegops divaricata (Cope). R. 2668. Drawing of the specimen figured in Pl. II. fig. 3. × 1·03.

which during life stood out as a backwardly projecting bony flange over the otic notch. The circumorbital bones are all present. The postorbital has a ventral rounded edge which fits into a notch in the jugal. The lachrymal is excluded from the nostril. The external nares are perfectly shown. The premaxilla is small; it is slightly displaced, so that the premaxilla-maxillary suture is shown. The maxilla bears a series of small homodont teeth. In this form the quadrate is ossified, and in this specimen is still in sutural contact with the squamosal, but displaced somewhat backwards.

The orbits are oval, widely separated, and placed in the middle of the skull length. Sclerotic plates and a number of small scattered supraorbital plates are present. The latter bear an ornament of fine tubercles. Heavy bony ridges on the skull follow the course of the lateral line system, *e. g.* occipital commissure, supra-orbital canal, etc. On these ridges pits mark the openings of the tubuli which connect the underlying canal with the surface.

The ornament of the cranial bones is coarse and consists of strongly developed radiating ridges and tubercles (Pl. II. fig. 3). This agrees with the heavy ossification of the skull, the enclosure of the lateral line canals in bone, and the presence of spines on the tabular and lower jaw.

The lower jaw is preserved as an impression of the external surface. The ornament of the dentary consists of longitudinal striations which in no way resemble the heavy course markings on the dermal bones. The dentary appears to form the entire external surface of the anterior part of the jaw, and extends back almost to the articular surface. The tooth-bearing edge is incompletely preserved, so that no teeth are visible. Two other bones of the lower jaw are clearly shown. The angular corresponds with that of R. 2546 running along the lower edge of the jaw and bearing on its ventral margin two spines. The surrangular is small, crescentic shaped, the dorsal surface is convex, and this depression marks the articulation for the quadrate; from the convex posterior margin projects three spines.

The second specimen R. 2546 (Pl. II. fig. 2) represents a complete skull in which the individual bones, although slightly displaced, are clearly shown, and the absence of the lower jaw on one side allows of the complete determination of the structure of the palate.

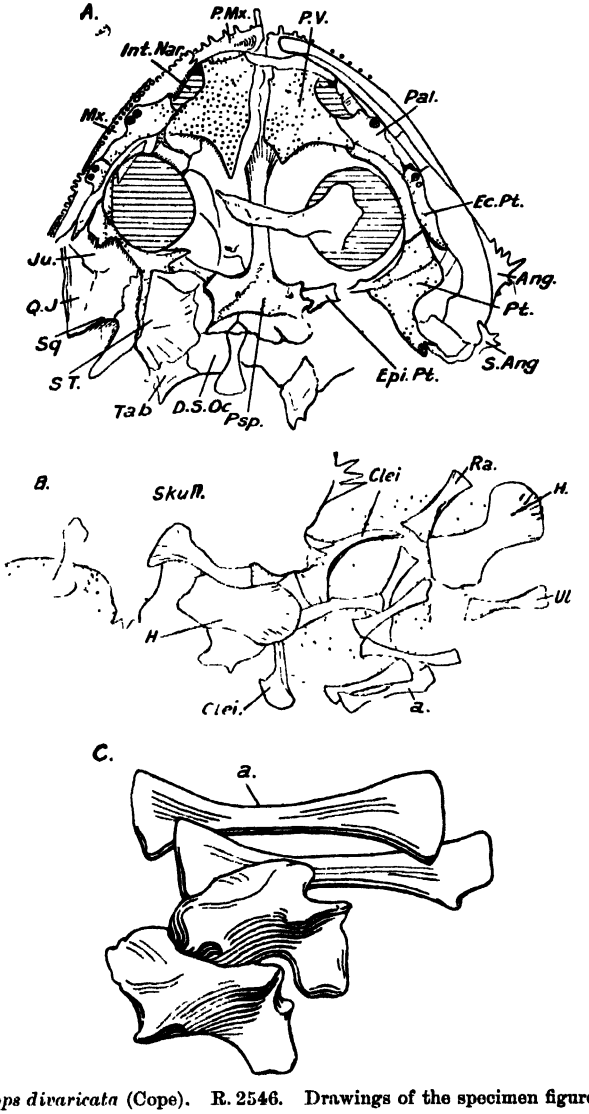
The right premaxilla (text-fig. 9) stretches back to the anterior border of the internal nares. It carries five small teeth at the base of which several small foramina are present. These foramina served for the terminal distribution of blood-vessels and nerves. From the internal nares the maxilla extends along the margin of the skull for some distance, but it is incomplete posteriorly. It also bears a series of small teeth. The anterior part of the maxilla forms the outer border of the internal nares and extends dorsally as a convex flange to form the lateral wall and part roof of the nares. The border of the internal nares is completed by the prevomer and palatine. The prevomers extend to the mid-line of the palate and overlie ventrally the processus cultriformis of the parasphenoid. They are heavily tuberculated. The palatines also bear numerous tubercles and in addition carry two large tooth pits. The ectopterygoid extends behind the palatine and between the maxilla and pterygoid. It bears tubercles, but there is also a tooth and its replacement pit present. The pterygoid of one side only is complete; it extends forward to meet the prevomer, so that the palatine is excluded from the interpterygoid vacuity margin. The inner margin of the pterygoid which bounds this vacuity is smooth and gently curved. Both palatal and quadrate rami are covered with tubercles. The facet for articulation with the basipterygoid process of the parasphenoid stands out as a process from the quadrate ramus and is jagged in appearance, so that the union was a sutural one. Between the pterygoids and the parasphenoid, and present on both sides, lie two small bones, which may be regarded as the epipterygoids. They are stout, columnar, and present a convex surface.

The parasphenoid is small; the basal part forms a broad short plate, while the processus cultriformis is wide and flat. The basipterygoid processes are stout and broad, and their lateral articulating faces are deeply convex. Two carotid foramina are present at the posterior ends of grooves which cross the base of the processes. The palate posterior to the parasphenoid is not preserved. The quadrate is ossified, so that a restoration (text-fig. 10) of the palate can be made. I have omitted in the figures the numerous octagonal bony plates covered with tubercles that lie scattered in the wide interpterygoid vacuities (Pl. II. fig. 2). They are exceedingly numerous, do not articulate with one another, and represent dermal ossifications in the palatal roof.

The bones of the skull-roof are shown as impressions of the inner surface as seen through the interpterygoid vacuities, and confirm the structure of the skull-roof shown in the first specimen (R. 2668). Here the posterior part of the table of

the skull is preserved. The dermo-supraoccipitals are rectangular bones lying behind the parietal region. Tabulars are present on both sides, and their free lateral margin carried three spines. The two free margins slope upwards and

Text-figure 9.



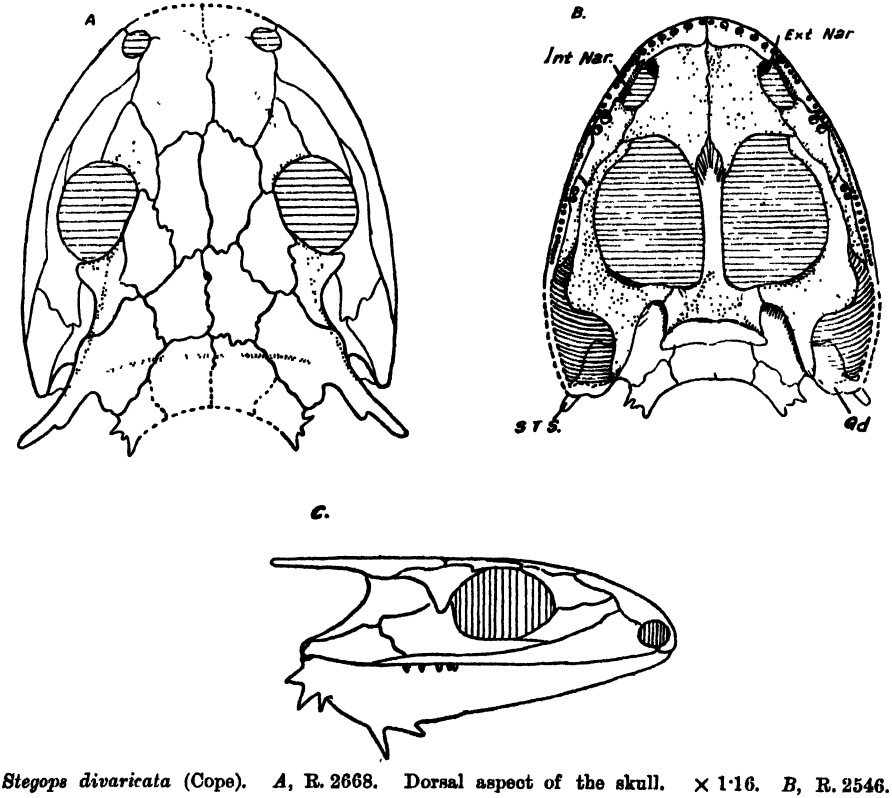
Stegops divaricata (Cope). R. 2546. Drawings of the specimen figured in Pl. II. fig. 2. A, × 1·3; C, × 3·6.

inwards as two ridges between which a groove lies; this receives the paroccipital process. The supratemporal is large and is continued posteriorly, as in the previous specimen, as an elongate spine which projects backwards as a free outstanding

process over the otic notch. Quadratojugal, squamosal, postfrontal, and post-orbital are partly shown. The ossifications in the palatal roof unfortunately make the recognition of further structure impossible.

In the lower jaw the surangular is a small crescentic-shaped bone whose dorsal surface is deeply concave. From the posterior convex margin projects three spines. The angular extends along the outer ventral margin of the jaw as a narrow boat-shaped bone bearing on its hinder margin a series of six spines. This specimen differs from the previous specimen in the number of spines carried on the angular,

Text-figure 10.



Stegops divaricata (Cope). *A*, R. 2668. Dorsal aspect of the skull. × 1·16. *B*, R. 2546. Restoration of the palate. × 1·08. *C*, R. 2668. Right lateral aspect of the skull and lower jaw, maxillary teeth incompletely represented.

in this case six (*cf.* two). This may be either imperfect preservation or simply a growth difference.

The restoration of the dorsal surface of the skull (text-fig. 10) is based on specimen R. 2668; the posterior margin of the table of the skull is taken from the second specimen, R. 2546.

Associated with the skull (R. 2546) are several limb bones, ribs, and scales (text-fig. 9). The ventral scales are smooth, oval, some 3 mm. in length and 0·5 mm. broad, with a thickened hinder end. Fragmentary remains of dorsal scales are also present. Ribs are straight, slender, and expanded at both ends. Two humeri,

which have been completely flattened, and what is presumably a radius, an ulna, and a cleithrum are also preserved.

The vertebral column is represented by two neural arches with, in addition, scattered triagular elements which resemble the similar structures in *Erpetosaurus radiatus* and in the specimen of Phyllospondylian remains (R. 2664) (see Pl. IV, fig. 2). These latter structures present a smooth or roughened surface, and it is suggested that they represent posterior neural arch elements which are incompletely ossified. The neural arch elements (text-fig. 9) are elongated antero-posteriorly with low neural arches and well-marked pre- and post-zygapophyses. The transverse processes are turned down ventrally, flattened and seen in side view. These are broad and carried nearer the anterior face of the vertebra.

Genus PLATYRHINOPS, gen. n.

PLATYRHINOPS MORDAX (Cope).

Cope, 1874, Trans. Amer. Phil. Soc. xv, p. 274 (*Tuditanus mordax*).

Material:—

R. 2670. Impression of external surface of skull (Pl. III. fig. 1; text-figs. 11, 13, A).

R. 2670. Counterpart slab of the same individual skull with impression of the palate (Pl. III. fig. 2; text-fig. 12, 13, B).

Measurements:—

Length of orbit, 14 mm.; breadth of orbit, 12 mm.; interorbital distance, 18 mm.; length of skull preserved in median line, 40 mm.; breadth of table of skull, 20 mm.

The impression of the skull of *Platyrhinops mordax* is incomplete anteriorly. That the muzzle is blunt and rounded is indicated both on this and on the counterpart slab. The outline of the orbits is distinctly preserved; these are large and oval. Within the orbits bony plates of two types are visible. The supraorbital series bear an ornament similar to that of the skull bones. The remaining plates bear fine tubercles and represent palatal ossifications.

The general structure of the skull-roof is shown in text-figs. 11 and 13, A. The nasals are incomplete. Here, as in the Genus *Steyops*, both nasals and frontals are larger than the parietals.

The posterior margin of the skull is formed by the tabulars and dermo-supraoccipitals. The tabulars are small triangular bones attached to the posterior margin of the supratemporal bone; they have a very short suture with the dermo-supraoccipital. The posterior margin of the table of the skull is deeply concave. The supratemporal bone extends forward lateral to the parietal to reach the post-frontal. A considerable part of the lateral margin is free, and forms the dorsal margin of the wide otic notch.

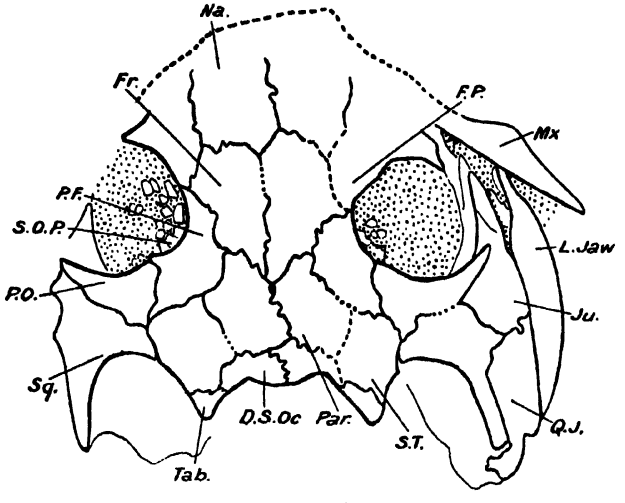
The circumorbital series of bones is incomplete. The postorbital ends ventrally in a blunt process which fits into a notch on the jugal. The posterior margin of the squamosal is deeply excavated to form the wide shallow otic notch. The quadrato-jugal extends posterior to the squamosal. Impressions of the ossified quadrate region are present behind the otic notch, but these show no certain structures.

The ornament is very regular and even in appearance, and is shown on the plate. It consists of fine regular pitting, the intervening bone standing out as a honeycomb structure.

The presence of both lower jaws (text-fig. 12) over the margin of the palate obscures the structure of this region. The prevomers are two bony plates, that of

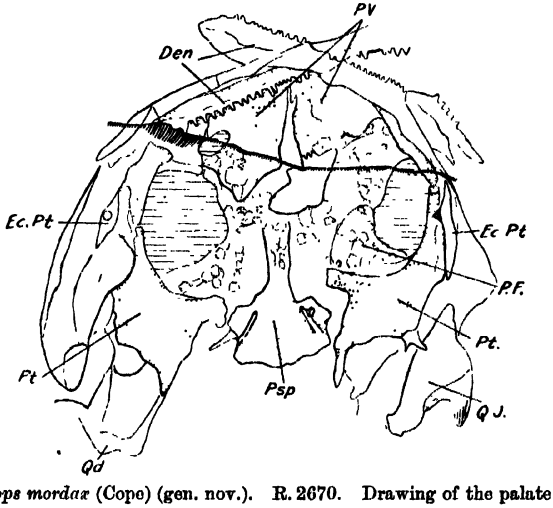
the right-hand side forms the anterior and lateral margins of the internal nares. They are heavily tuberculated, and while distinctly one bone, have the appearance, especially near the margin of the pterygoid vacuity, of being overlaid by small

Text-figure 11.



Platyrhinops mordax (Cope) (gen. nov.). R. 2670. Drawing of the dorsal surface of the skull figured in Pl. III. fig. 1. × 1·16.

Text-figure 12.



Platyrhinops mordax (Cope) (gen. nov.). R. 2670. Drawing of the palate figured in Pl. III. fig. 2. × 1·08.

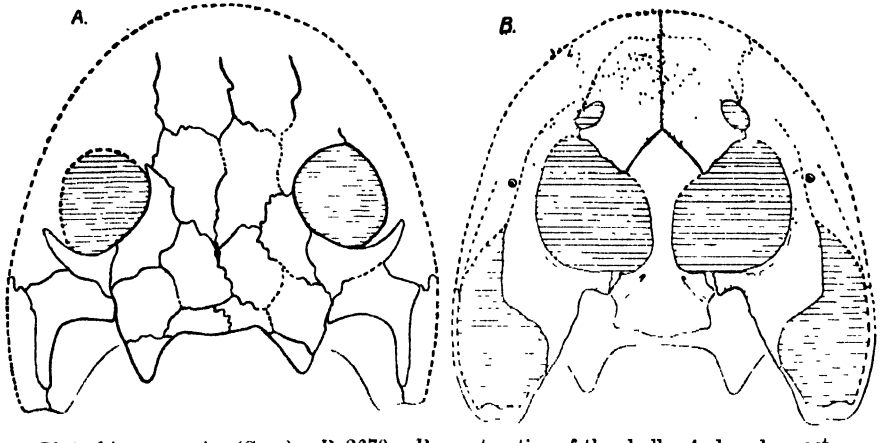
octagonal plates. That the anterior part of the processus cultriformis, which rests on the dorsal surface of the prevomers, is broad, is suggested by the wide divergence of the prevomer-parasphenoid sutures. The posterior part of the processus

cultriformis is slightly convex, and widens at its base into the flat posterior plate. The basipterygoid processes are broad and form sutural unions with the pterygoid. Two carotid foramina are present, and from these grooves extend round the base of the processes.

The pterygoids are heavily tuberculated. The palatal ramus, which is broad and flat, is incomplete anteriorly, but must have reached the prevomer. The margin which bounds the interpterygoid vacuity shows a smooth narrow band. The processes for articulation with the parasphenoid project from the quadrate ramus towards the mid-line. Fragments of both ectopterygoids are present. These are untuberculated, carry a single large tooth, and have a characteristic ornament.

The quadrates are ossified. The length between the quadrate and the hinder margin of the parasphenoid or the table of the skull is considerable, so that the condyle must be situated some distance in front of the articulation of the lower jaw.

Text-figure 13.



Platyrhinops mordax (Cope). R. 2670. Reconstruction of the skull; *A*, dorsal aspect and *B*, palate. × 1.

Scattered over the palate are numerous small octagonal bony plates, which carry tubercles. They resemble the palatal ossifications of *Stegops divaricata*.

The lower jaw is fragmentary. The dentary is displaced and bears a continuous series of small bluntly conical teeth which are anchylosed to the bone. The external surface of the dentary is tuberculate. Below the dentary, and posteriorly, the lower jaw presents a smooth surface. There is an angular present; it is an unornamented strip of bone running along the ventral hinder border of the jaw.

A new genus has been erected for this species for the following reasons. It is clearly a Phyllospondyl.

While sharing with the genus *Stegops*:

(*a*) the presence of parietals smaller than the frontals or nasals,
(*b*) the occurrence of numerous ossified plates in the palate roof,
(*c*) the broad-nosed skull,
(*d*) the position of widely separated orbits in the middle of the skull length,

it is generically distinct for the following reasons:

1. There are no spines present on the tabulars or on the lower jaw,
2. The supratemporal bears no large spine as in *Stegops divaricata*.

Genus Mytaras, gen. n.

Mytaras macrognathus, sp. nov.

Material:—

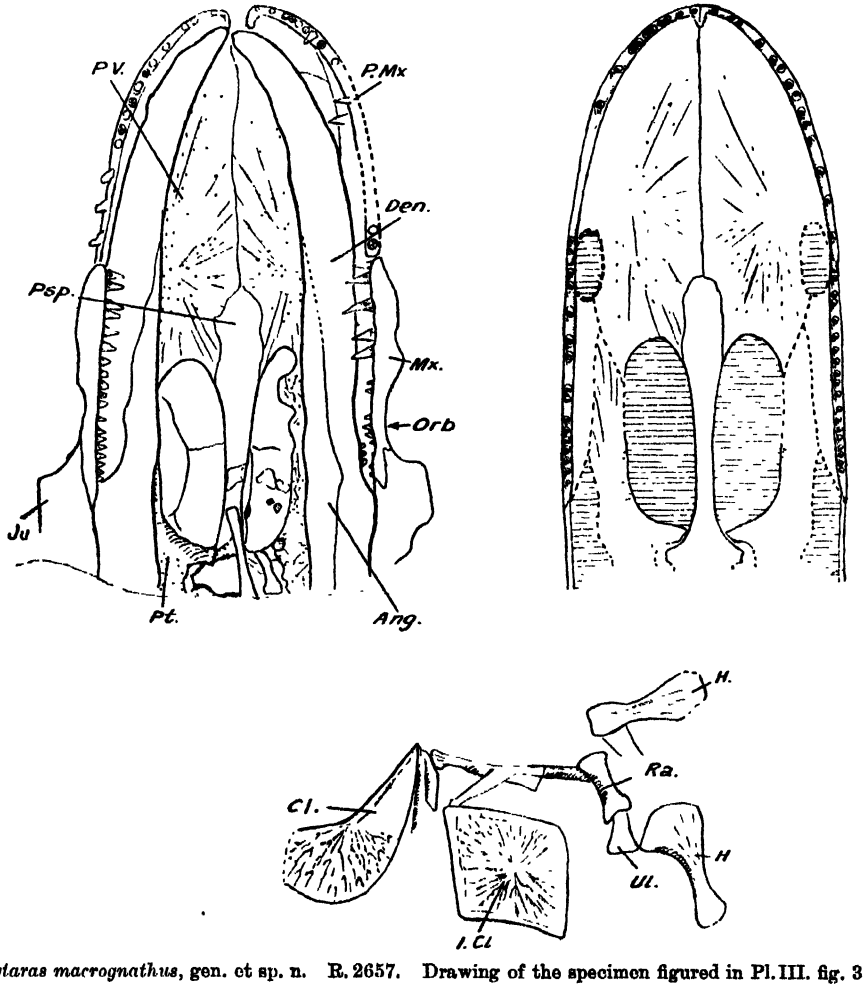
R. 2657. Impression of palate, lower jaw, part of the cheek, shoulder-girdle, and limbs (Pl. III. fig. 3; text-fig. 14).

Measurements:—

Length of orbit, 10 mm.; length of lower jaw preserved, 60 mm.

Specimen R. 2657 represents an animal very different to any yet described and

Text-figure 14.



Mytaras macrognathus, gen. et sp. n. R. 2657. Drawing of the specimen figured in Pl. III. fig. 3, Reconstruction of the palate. × 1·19. Interclavicle, clavicle, and fore limb. × 1·73.

is regarded as a new genus and species. The skull is elongate and almost parallel-sided. All the peculiarities of the skull are correlated with the increase in length of the pre-orbital region.

The structure of the palate is incompletely shown, as the presence of both lower jaws entirely covers all the bones between the margin of the pterygoids and the skull-edge (text-fig. 14). The premaxillæ are unusually long. The ventral surface is shown on both sides and bears a succession of teeth and pits; although not constant, tooth and pit usually alternate. The maxillæ are displayed in side view, their upper edges being rotated outward. The marginal teeth are large, acutely pointed, and show a longitudinal striation, which continues more than half-way up the tooth. The dorsal border of the maxilla forms part of the ventral margin of the orbit; this orbital margin is continued by the jugal. Posteriorly the jugal is incomplete, but it forms part of the ventral border of the skull for some distance.

Some of the sutures of the cranial bones are seen on the inner surface through the interpterygoid vacuities. The parietals are elongate, the pineal foramen is present, and is situated near the posterior margin. There is a postfrontal bone present, so that the parietal or frontal did not enter the margin of the orbit.

The parasphenoid is partially obscured by two extraneous bones which lie across it, and the specimen is broken short behind. The left basipterygoid process is completely hidden, but that of the right side stands out from the parasphenoid as a flat process. There are no traces of carotid foramina. At the base of the processus cultriformis is a small triangular tuberculated patch. The processus cultriformis is wide and flat; anteriorly it rests on the dorsal surface of the prevomers. The latter extend over the anterior palatal surface and are in this species very large. They are covered with small tubercles which have a delicate radial arrangement, quite unlike the heavy tuberculation of the pterygoids. Both the pterygoids are shown in part. The margin of the interpterygoid vacuity of the right side is incomplete. There is a smooth face sloping to this margin, but otherwise the palatal ramus is heavily tuberculated. The quadrate ramus appears stout, but is broken off short posteriorly. The articulating face for the basipterygoid process of the parasphenoid is borne on the smooth upturned margin.

The internal nares are not visible, but must have been situated far back, and were probably elongate oval slits.

The ornament has a delicate smooth regular appearance (Pl. III fig. 3).

Lower jaw.—The dentary forms the external surface of the anterior ramus of the jaw. No teeth are shown. The angular is also incomplete, but extends below the dentary for some distance. The ornament on the jaw resembles that of the maxilla and jugal etc., and is shown on the plate. There are no traces of lateral line canals here or on the skull bones.

Pectoral girdle.—The shoulder-girdle is represented by an interclavicle and clavicle. The interclavicle is a rhomboidal bone, bearing a radial ornament which does not reach to the margin of the bone. The clavicle of one side only is present. It is also in part ornamented; dorsally the surface is smooth and is the overlap margin for the cleithrum. Two humeri, a radius and an ulna, are present, and numerous scales. The ventral scales are smooth, in length 2 mm. and 0·5 mm. broad. Fragments of oval dorsal scales are also present which show a concentric ornament.

The genus *Mytaras* is founded for the single specimen of the species *Mytaras macrognathus*, which in the peculiar elongation of the pre-orbital part of the skull, and the slender almost parallel-sided skull, is totally distinct from all the described species.

Genus Pelion Wyman, 1868.

Cope, 1868, Proc. Acad. Nat. Sci. Phil. 211.

Pelion lyelli Wyman.

Wyman, 1858, Amer. Journ. Sci. (2) xxviii, p. 160.

Material:—

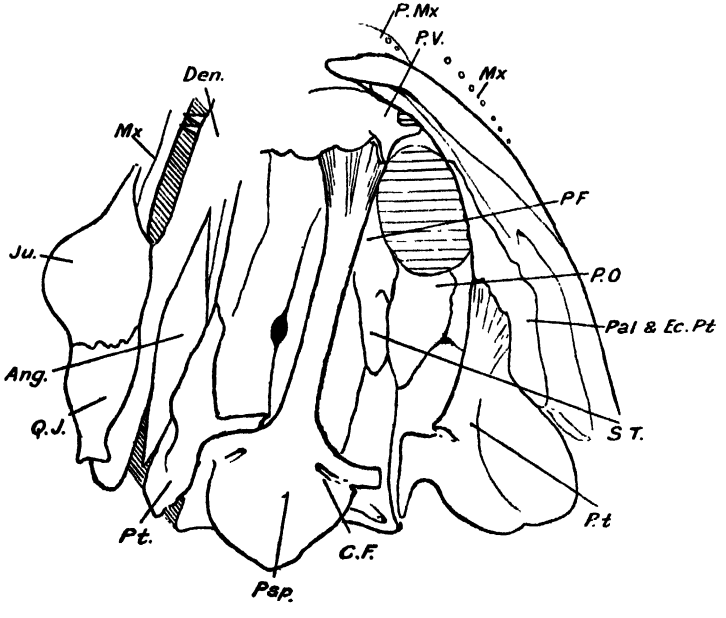
P. 2674. Impression of the palate, dorsal surface of the skull shown (Pl. IV. fig. 1; text-figs. 15, 16).

Measurements:—

Length of skull, 23 mm.; length of orbit, 6 mm.; breadth of orbit, 6 mm.; interorbital distance, 6 mm.; width of table of skull, 16 mm.; length of lower jaw, 24 mm.

P. 2647 is a very complete impression of the palate, and of the inner surface of the skull-roof (text-fig. 15). The skull is small, and shows a palate, which, while in plan essentially similar to the other types of this group, is very different in detail.

Text-figure 15.

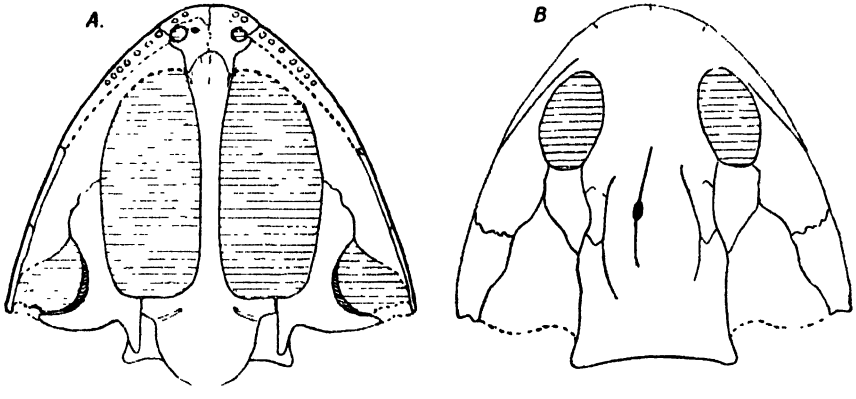


Pelion lyelli Wyman. P. 2674. Drawing of the specimen figured in Pl. IV. fig. 1. × 2·86.

The parasphenoid is flat, and posteriorly expands as a wide plate which resembles the parasphenoid of *Eugyrinus wildii* and that of the Branchiosaurs more than the smaller rectangular and more T-shaped parasphenoid of *Erpetosaurus radiatus*, *Stegops divaricata*, etc. This plate is flat and smooth, bearing towards the margin a faint radial ornament. The basipterygoid processes are well developed, and project laterally as wide flat processes. Two carotid foramina are present, and grooves run from these foramina to the posterior margin of the basipterygoid processes. The processus cultriformis is wide and flat. The prevomers are displaced, so that the grooved faces for articulation with these bones are exposed. The pterygoid of the left-hand side is complete, but shows one clean fracture. The shape of the bone is curious. The palatal ramus is flat and smooth. There is no definite process to articulate with the basipterygoid processes of the parasphenoid, but the pterygoid forms a lateral antero-posterior projection, apering posteriorly, which sits flat against the basipterygoid process of the

parasphenoid. The surface of the quadrate ramus is slightly pitted, lying lateral to the pterygoid, and on its outer margin there is a curious wide delicate flange of bone, which is also part of the pterygoid. When in the correct position, it projects ventrally from the palate as a thin sheath of bone to cover the inner surface of the masticatory muscles which pass through the subtemporal fossa. A pterygoid of a similar type occurs in *Palæogyrinus decorus*. To the anterior surface of the pterygoid is attached a bone which bears a deep, coarse, irregular ornament of grooves and pits. There is no suture visible, but this bone must represent both palatine and ectopterygoid. The margin of the interpterygoid vacuity is carried forwards by the palatine for some distance, but it is incomplete anteriorly. The prevomer shown on the left-hand side is small and sends out a small process laterally over the palatine. On front of this process it is excavated to form the margin of the internal nares. The premaxilla and maxilla are represented only by the impressions of the teeth which they carried. The premaxillæ are small. The marginal teeth are small, conical, and acutely pointed. The anterior two maxillary teeth show longitudinal striation of the enamel towards the apex of the teeth.

Text-figure 16.



Pelion lyelli Wyman. *A*, P. 2674. Reconstruction of the palate; *B*, dorsal aspect of the skull. × 2·6.

The margin of the cheek is completed by jugal and quadrato-jugal whose external surface is shown on the right-hand side of the specimen. The jugal appears to enter into the margin of the cheek. Both quadrato-jugal and jugal bear a strong ornament of radiating ridges; a few tubercles are present near the centre of radiation.

The sutures of the inner surface of the skull-roof are visible through the interpterygoid vacuities. The orbits are placed far forward and are well separated. The postorbital bones are elongated antero-posteriorly. There is an intertemporal bone present, a primitive feature retained in no other Linton species except *Branchiosaurus*. The tabulars are small and are grooved parallel to their posterior margin for the reception of the paroccipital process.

Both lower jaws are present, but only the dentary and angular are shown. The dentary bears an ornament of elongate tubercles. Splenials are present. The angular of the right jaw appears as a boat-shaped bone and bears a radial ornament of ridges.

There are no body-remains associated with the skull. Sclerotic plates are present in the orbit.

KEY TO THE DETERMINATION OF THE

(The lines indicate that this

	Erpetosaurus radiatus (Cope).	*Erpetosaurus laevis* (Moodie).	*Colosteus scutellatus* (Newberry).
SKULL.			
Position of orbits	Anterior to mid point of skull length. Inter-orbital width less than width of orbit.	Anterior to mid point of skull length. Inter-orbital width less than width of orbit.	Anterior to mid point of skull length. Inter-orbital width greater than width of orbit.
Orbital ossifications	None known.	None known.	None known.
Parietals	Form a single bone.	Form a single bone.	
Supratemporal			
Posterior margin of table of skull.	Concave.	Concave.	Very slightly concave.
Lateral line grooves	None.	———	Deep grooves present
PALATE.			
Articulation of pterygoid and parasphenoid.	Movable.	Movable.	
Palatine	———	Enters interpterygoid vacuity margin.	
Tuberculation of palate	Pterygoid.	Pterygoid only.	
Teeth	———	Premaxillary teeth large Maxillary teeth small and homodont. Dentine ridged.	Palatal teeth large. Premaxillary and maxillary teeth smaller. Acutely pointed, with very characteristic longitudinal ridging of the dentine.
Palatal ossifications	(?) Present.	Stated by Romer to be present in one of his specimens.	
Vertebræ	Vertebral plates present throughout vertebral column.	———	———
Scales	Ventral scales elongate smooth parallel-sided with rounded ends (10 mm. by 5 mm.). Dorsal scales fragile, showing a concentric radial ornament.	———	Ventral rhombic scales are stated by Romer to be present.
CHARACTERISTIC OF THE SPECIES.	Parietals form a single bone. Type of palate, *e.g.*, movable articulation of pterygoid and parasphenoid, etc.	Distinguished from the previous species by:— 1. Different proportions of skull. 2. Presence of carotid foramen on the parasphenoid (see text). Pterygoid only tuberculate.	Form and character of the teeth; especially the presence of a large tooth on the extreme anterior end of the dentary with a groove on the external surface of the dentary immediately behind it. Presence of lateral line grooves.
	Interorbital width less than width of orbit. Preorbital region narrow.		Interorbital width greater than width of orbit.
	Skull long and high. Orbits situated in anterior half of skull length.		

region of the skull is not known.)

Stegops divaricata (Cope).	*Platyrhinops mordax* (Cope).	*Mytaras macrognathus.*	*Pelion lyelli* Wyman.
In middle of skull length. Interorbital width greater than width of orbit.	In middle of skull length. Interorbital width greater than width of orbit.	In posterior half of skull length.	In anterior half of skull length. Interorbital width greater than width of orbit.
Sclerotics and supra-orbitals.	Supraorbitals.	—	Sclerotics.
Small compared to frontals and nasals.	Small compared to frontals and nasals.	—	—
Large, continued posteriorly as a free spine which stands out over the otic notch.	Large, no spine present.	—	—
Concave. Tabular bears three spines.	Deeply concave	—	Slightly concave.
Encased in prominent bony ridges.	None.	—	—
Sutural.	Sutural.	Movable.	Movable.
Does not enter interpterygoid vacuity margin.	Does not enter interpterygoid vacuity margin.	Does not enter interpterygoid vacuity margin.	Enters interpterygoid vacuity margin.
Pterygoid prevomer, palatine, ectopterygoid, and parasphenoid.	Pterygoid prevomer, palatine, and parasphenoid, Ectopterygoids ridged ornament.	Pterygoids and prevomer; also few tubercles on the parasphenoid.	Palatine bears ridged ornament.
Premaxillary and maxillary teeth small. Bluntly conical. Smooth.	Premaxillary and maxillary teeth small. Bluntly conical. Smooth.	Premaxillary and maxillary teeth acutely pointed. Dentine edged.	Premaxillary and maxillary teeth slender and pointed
Present.	Present.	None.	None.
Well-ossified neural arches and vertebral plates.	—	—	—
Ventral scales small (3mm. by 0·5 mm.), parallel-sided with rounded ends, and thickened hinder margins, smooth. Fragmentary dorsal scales with concentric ornament also present.		Ventral scales oat-shaped (2 mm. by 0·5 mm.), small, smooth or with faint striæ. Fragmentary oval dorsal scales with concentric ornament also present.	—
Presence of palatal ossifications. Tuberculation of all the palatal bones. Lateral line grooves encased in bone.	Presence of palatal ossifications. Tuberculation of all the palatal bones except the ectopterygoid, which bears a ridged ornament. Ornament of skull bones.	Ornament of the cranial bones. Type of palate, *e. g.*, very large prevomers, etc.	Absence of tuberculation on the palatal bones. Presence of ventral flange from the pterygoid.
Spines on supratemporal, tabular, angular, and surangular.	Complete absence of spines.		
Skull broad and flat. Orbits in middle of skull length, and interorbital width greater than width of orbit.		Preorbital region of skull very elongate, *i. e.*, orbits situated in posterior half of skull length.	Skull broad and flat. Orbits situated in anterior half of skull length.

The description of this specimen of *Pelion lyelli* differs materially in several respects from the description given by Romer of the same species. In the British Museum specimen the structure of the parasphenoid is clearly shown, and there is no doubt that posteriorly it extends as this curious shaped plate. The pterygoid is also more completely shown in the B. M. specimen and has an unusual, although not unique, structure. Both palatine and ectopterygoid here bear an ornament of irregular coarse grooves. No palatal teeth are preserved in this specimen.

Order LEPOSPONDYLI Zittel.

Genus OPHIDERPETON Fritsch.

Fritsch, 1899-1901, Fauna der Permformation Bohmens, Bd. 4.

OPHIDERPETON AMPHIUMINUS (Cope).

Cope, 1868, Proc. Philad. Acad. Nat. Sci. p. 218.

Material:—

P. 2673. Impression of roof of skull, lower jaw, vertebral column, ribs, and scales (Pl. V. figs. 2, 3; text-figs 17 A, C).

R. 2657. Impression of lateral surface of the skull, lower jaws, one bone of shoulder-girdle, scales (Pl. V. fig. 1; text-fig. 17, B, C).

Skull R. 2657. Length of maxilla, 20 mm.; length of premaxilla, 8 mm.; length of jaw, 53·2 mm.; depth of jaw, 8 mm.; length of orbit, 11 mm.; depth of orbit, 5 mm.

P. 2673. Width of table of skull, 11·5 mm.; length of jaw preserved, 45 mm.; depth of jaw, 8 mm.

P. 2673 is an impression of the skull and part of the vertebral column. In the skull (fig. 17, A) the pre-orbital part is missing, and the neural cranium, premaxilla, and maxilla have been lost. While the cranial roof is complete posteriorly, the arrangement of the bones is quite unlike the more primitive generalised pattern of the skulls of the other Amphibia in this fauna. The median roofing bones are represented by two pairs. The more anterior pair is elongate, with almost parallel sides, and unites with the posterior pair by an interdigitate suture. The posterior pair of bones present a smooth posterior edge, which forms a part of the hinder margin of the table of the skull. The length of the lower jaw (which is incomplete) suggests that there is a considerable length of skull anterior to that preserved. Further the premaxillæ retained in the specimen R. 2657 are small. It is therefore suggested that the long bones are frontals and the smaller posterior pair parietals. The inclusion of the minute pineal foramen in the frontals is unusual, but not unparalleled.

The roof of the skull is completed by two bones lying lateral to the frontals and parietals, which represent the remains of the temporal row of bones and are presumably supratemporal and tabular. Wedged in between tabulars and parietals lies a small triangular bone which is the dermo-supraoccipital. The position is an unusual one and must result from the modification in structure in this skull. All these bones, supratemporals, tabulars, dermo-supraoccipitals, frontals, and parietals form a roof to the skull with a distinct projecting lateral edge.

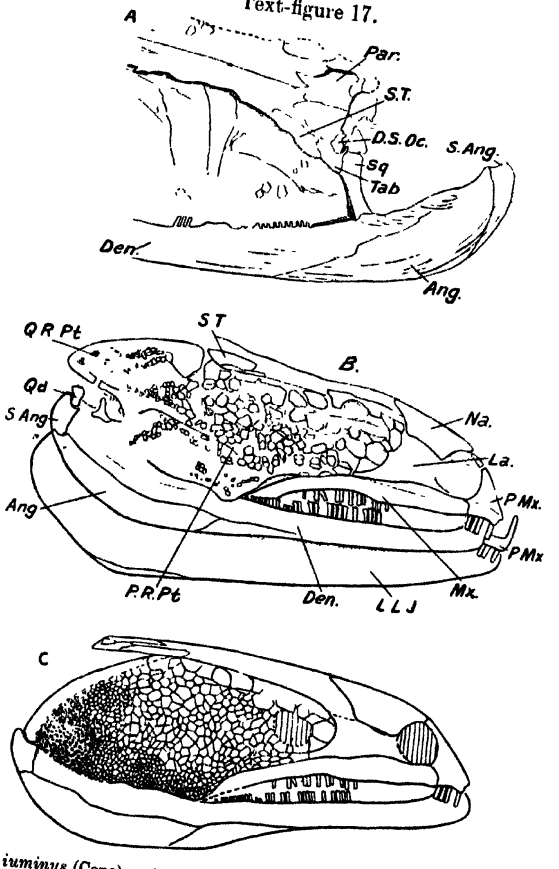
Of the cheek-bones of the skull only a posterior pillar remains, which I propose to call squamosal. Scattered granulated scales (of which the largest is 2 mm. across) suggest that the cheek-bones, as in R. 2657, are replaced by small scales lying in the dermal layer of the skin.

The ornament on the dermal bones consists of a few pits which seem to show radial distribution.

The lower jaw is long, broad, and curves up bluntly behind to the articulation

for the quadrate, which is a small deep depression. The shape of the jaw is characteristic and easily recognised. Both angular and surangular are small, the angular bearing a marked ornament. The dentary is well defined, the surface is

Text-figure 17.



Ophiderpeton amphiuminus (Cope). *A*, P. 2673. Drawing of the skull figured in Pl. V. fig. 2. × 1·46. *B*, R. 2657. Drawing of the skull figured in Pl. V. fig. 1. × 1·94. *C*, Restoration of the skull, lateral aspect, based on the specimens in A & B.

smooth but shows faint longitudinal striæ. The dentary teeth are erect, cylindrical, and show no enlargement of their bases, and the enamel is smooth. They tend to be associated in pairs. The shape of the lower jaw and the character of the teeth are characteristic of the genus.

Vertebræ and Ribs, etc. (Pl. V. fig. 3).

Part of the vertebral column of this long slender-bodied animal is preserved. All the vertebræ are alike, and the resemblance of the vertebræ and the ribs to those of the Nurschan species of Ophiderpeton has already been pointed out by Romer.

The body of the centrum is well ossified and shows a ventral medial ridge which broadens at either end; on each side of this ridge the centrum is concave. The transverse processes are broad and flat and stand out laterally from the neural arch. There is no neural spine. Well-developed pre- and post-zygapophysis project antero- and postero-laterally from the body of the neural arch.

The ribs are forked with dorsal and ventral spines, and are long, slender, and taper at the free end to a point. The head of the rib which articulates with the transverse process is broad and flat. The dorsal spine ends abruptly a some distance from the rib-head and shows a pit.

The ventral dermal armour consists of long narrow scales (4–5 mm.) which, when in position, overlap one another. In the dorsal and lateral surface of the animal small oval scales of various sizes occur; these lie scattered over the vertebral column.

In the second specimen R. 2627 (Pl. V, fig. 2), a lateral impression of a skull and part of the post-cranial dermal armour is preserved.

Both premaxilla and maxilla are present (text-fig. 17, B). The premaxilla is small and bears teeth larger than the maxillary teeth, but resembling them in the cylindrical form and smooth enamel. The maxilla is slender and stretches back to the pterygoid, and the anterior dorsal margin is grooved. Premaxilla, maxilla, and dentary carry a number of isolated pits, which on the maxilla and on the anterior part of the dentary are arranged longitudinally. A lateral impression of the roofing bones of the skull is present, but the individual bones are not shown. There is a separate nasal bone above the premaxilla. Of the rest of the skull-roof the specimen shows the table of the skull to be slightly arched and to have a distinct lateral edge. An impression of the orbit is retained; this is placed very far forwards.

The cheek is covered by a series of small plates. The anterior plates are large irregularly pentagonal or hexagonal in form, and there is a series of large plates over the eye, towards the back of the skull they decrease in size to minute tiny scales. Where undisturbed these ossifications form a continuous surface *.

The pterygoids are massive and extend to the posterior margin of the maxilla. In the articular surface of the lower jaw sits a small waisted bone which is the quadrate. The squamosal is not preserved. Both lower jaws are present and exhibit the very characteristic shape. The dentary bears no ornament; the dentary teeth tend to be associated in pairs, and are peg-like and cylindrical. The surangular is ornamented.

Two narrow splint-like bones represent the shoulder-girdle. These are the clavicle and the cleithrum. The ventral scales, as in the previous specimen, are long and slender. They overlap one another to form a rhomboidal pattern and commence immediately behind the pectoral girdle. The dorsal surface was covered with very small scales irregular in size and form. Small scales† are present anterior to the shoulder-girdle; these represent secondary dermal ossifications.

The restoration of the skull (text-fig. 17, C) is based on the specimens P. 2673, R. 2657.

* A skull of *Ophiderpeton brownriggii* in the National Museum of Ireland, Dublin, shows that in this species, as in *Ophiderpeton amphiuminis*, the cheek region consists of numerous small polygonal plates.

† The dermal armour of Amphibia for which such names as abdominal rods, ventral scutellæ, dermosseous rods, etc., have been used, is in all cases identical. Further, the scales are homologous with fish scales and resemble them in their mode of articulation with one another. They are retained in Amphibia primarily on the ventral surface of the body, but there are no criteria for determining whether the dorsal scaling is primary or secondary. In many cases the number of scales is secondarily increased. The occurrence of scales anterior to the shoulder-girdle in Ophiderpeton denoted the presence of secondary dermal ossifications in this group.

Genus SAUROPLEURA Cope 1868.

Cope, 1868, Proc. Acad. Nat. Sci. Philad. p. 216.

SAUROPLEURA MARSHII (Cope).

Cope, 1869, Trans. Amer. Phil. Soc. xiv. p. 24 (*Colosteus marshii*).

SAUROPLEURA PECTINATA Cope.

Cope, 1868, Proc. Acad. Nat. Sc. Philad. pp. 216–219.

Material :—

SAUROPLEURA MARSHII (Cope).

R. 2659. Impression of dorsal surface of the skull, both lower jaws present. Thirteen dorsal vertebræ, ribs, ventral scales, and shoulder-girdle (Pl. VI. fig. 1; text-fig. 18, A).

SAUROPLEURA PECTINATA Cope.

R. 2653. Impression of lateral surface of the skull and both lower jaws. Vertebræ and shoulder-girdle. No ribs present (text-fig. 18, B).

R. 2656. Impression of skull, lower jaws (text-fig. 18, C).

R. 2651. Impression of palate, lower jaws. Dorsal vertebræ, shoulder-girdle, and ventral scales. No ribs present. Fore and hind limbs present (text-figs. 18 D, 20).

R. 2654. Vertebral column showing dorsal vertebræ, femur, and complete tail 9·9 cm. long (text-fig. 20).

Measurements :—

	Sauropleura marshii.	*Sauropleura pectinata.*			
	R. 2659.	R. 2653.	R. 2656.	R. 2651.	R. 2654.
Length of orbit	4·8 mm.	4·0 mm.	3·0 mm.		
Interorbital width	1 8 .		—		
Bd. of table of skull			6·0 ,,		
Lt. of lower jaw	19·5 ,,	17·0 ,,	24·0 ,,	22·5 mm.	
Lt. of clavicle	(?) 6·0 ,,	6·5 ,,	—		—
Av. bd. of scales	0·25 ,,	0·1 ,,		0·2 ,,	0·24 mm.
Av. ht. of centrum	2·9 ,,			—	1·2 ,,
Ht. of most ant. vert.		—		3·2 ,,	5·0 ,,
Ht. of most post. vert.		—	—	4·0 ,,	1·0 ,,

The British Museum material includes two species of *Sauropleura*. This conclusion was also reached by Romer after an examination of the American material. The value of the dermal armour as a characteristic of the species is doubtful, as the method of preservation often obscures its complete structure.

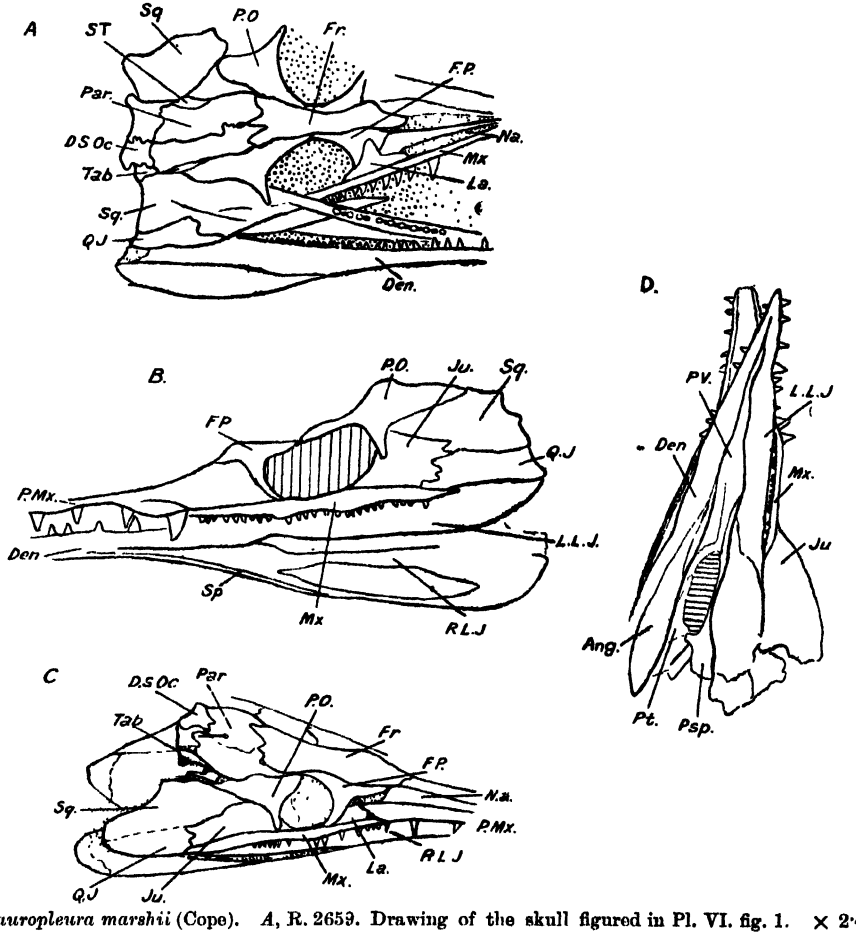
1. *Sauropleura marshii* (R. 2659) in which there is no marked difference in size between the premaxillary and maxillary teeth, but where these form a series gradually decreasing in size from the most anterior tooth; there is also an internasal space present, and the preorbital region of the skull is less elongate than in *Sauropleura pectinata*.

2. *Sauropleura pectinata* (R. 2656, R. 2651, R. 2653). There is a marked difference in size between the premaxillary and maxillary teeth. The premaxillary teeth are all large, those of the maxilla are small. The preorbital region of the skull is longer than in *Sauropleura marshii*. There is no evidence whether an internasal foramen is present or not.

Sauropleura marshii (R. 2659). The structure of the cranial roof of the skull is most completely shown in the specimen (R. 2659) of *Sauropleura marshii* (Pl. VI. fig. 1). All the sutures given are certain.

The dermo-supraoccipitals are two small bones lying posterior to the parietals. Behind the parietal and lateral to the dermo-supraoccipital is a small triangular bone, which is the tabular. That tabulars are present is confirmed in *Sauropleura*

Text-figure 18.



Sauropleura marshii (Cope). *A*, R. 2659. Drawing of the skull figured in Pl. VI. fig. 1. × 2·4. *Sauropleura pectinata* Cope. *B*, R. 2653. Lateral aspect of the skull (camera lucida drawing). × 4. *C*, R. 2656. Lateral aspect of the skull. × 1·71. *D*, R. 2651. Ventral aspect of the skull. × 2·64.

pectinata (R. 2656, text-fig. 18, C), where they lie as small triangular ornamented bones, lateral to the dermo-supraoccipitals. The parietals are oblong, rectangular, and include a small pineal foramen at the extreme anterior end of the medial suture. Lateral to the parietal and between the tabular and postorbital lies a small strip of bone which is the supratemporal. In this genus the frontals

together form a bone very characteristic in shape. It is waisted at the narrow interorbital region, and extends forward (between the nasals) to end in a blunt point. Here the nasals are interiorly incomplete, and between them lies a smooth unossified area, which in this specimen appears to be a genuine internasal space.

Of the circumorbital series of bones prefrontal, lachrymal, and a postorbital bone are preserved. The postorbital, which is analogous to the postfrontal and postorbital of other forms, extends forward dorsal to the orbit to meet the prefrontal bone.

The impression of the cheek is obscured by a superimposed impression of the lower jaw, but that this was relatively deep is shown. The sutures of the quadrato-jugal with the squamosal and jugal are distinct. The maxilla extends forward from the quadrato-jugal as a narrow bone and appears to enter the orbital margin. The premaxillary-maxilla suture is not obvious. A number of sharp pointed slightly recurved teeth are present. The right external nares is visible as a smooth depressed area lying between the maxilla, lachrymal, and nasal, and in front of the lachrymal. In the lower jaw the external surface of the dentary bears no ornament. The teeth are straight, acutely pointed, and associated in pairs. Tooth pits are visible on the ramus of the left jaw. The angular is a boat-shaped bone with a distinct radial ornament (Pl. VI. fig. 1).

SAUROPLEURA PECTINATA (Cope).

This species is represented by three skulls. R. 2653 (text-fig. 18, B) gives an impression of the cheek-bones of the skull, in which the relations of the post-orbital, squamosal, jugal, and quadrato-jugal are clearly shown. The maxilla is complete in this specimen, and the premaxillary-maxillary suture visible. The maxillary teeth are all small and quite unlike the large maxillary teeth of *Sauropleura marshii*. The preorbital region shows no certain structure.

R. 2656 (text-fig. 18, C) confirms the structures shown in the previous specimen. Here the parietals have slid over one another so that no pineal foramen is visible. The interorbital region is narrow and the frontals form a single waisted bone. The prefrontal, both in this specimen and R. 2653, has a longer ventral extension than in *Sauropleura marshii*. The preorbital region shows the nares to be represented by an elongate slit between the maxilla, lachrymal, and nasal; and the premaxilla-maxillary suture is confirmed. The maxillary teeth vary indiscriminately in size, but all are smaller than the large teeth of *Sauropleura marshii*. There is no gap between the nasals, so that an internasal space does not appear to occur in this species.

In the third skull (R. 2651, text-fig. 18, D) the anterior part of the palate is partially exposed between the lower jaws. The parasphenoid appears to be a wide flat plate which is very faintly ornamented. The processus cultriformis is convex ventrally and its expansion to the posterior plate is gradual. The interpterygoid vacuities are narrow and do not extend far anteriorly; the prevomers therefore are extensive bones.

The structure of the lower jaw, although preserved with all three skulls, is incompletely shown.

Shoulder-girdle.—Fragmentary remains of the clavicles and interclavicles are present. In no case is the complete form of clavicle or interclavicle shown.

Fore limb.—Two tiny humeri are present in the specimen of *Sauropleura pectinata*, R. 2651.

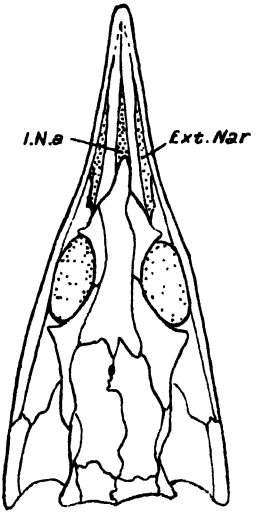
Hind limb.—With the exception of a femur present in R. 2651 and R. 2657, the hind limb in these specimens is not preserved. The proportions of the limbs with respect to body size is shown in text-fig. 20.

Dermal armour.—Scales pointed at both ends are present and overlap one another, forming a complete ventral armour. They commence immediately behind the pectoral girdle and do not persist behind the pelvic region. They are fine and

hair-like in *Sauropleura pectinata* (R. 2653), coarse in *Sauropleura marshii* (R. 2659), and in the specimen of *Sauropleura pectinata* R. 2657. In these specimens different regions of the body are preserved.

Vertebræ.—The dorsal series of vertebræ only is found in association with the skull. The neural spines are expanded and grooved to their distal margin. Towards the pelvic region they become taller and more slender, with well-marked

Text-figure 19.

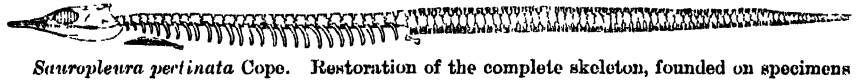


Sauropleura pectinata. Restoration of the skull, dorsal aspect. × 3·0.
I.Na., Internasal space.

grooves on the neural spines. The transverse processes are well developed. The centra show an hour-glass-shaped perforation which is superimposed on the impression.

The restoration of the complete skeleton of *Sauropleura pectinata* (text-fig. 20) is founded on specimens R. 2651 and R. 2654, in which the hind limbs are present. R. 2651 includes the complete anterior part of the body to the 1st or 2nd caudal

Text-figure 20.



Sauropleura pectinata Cope. Restoration of the complete skeleton, founded on specimens R. 2651, R. 2654. × 0·60 approx.

vertebra. The other specimen (R. 2651) exhibits a complete tail with a few of the presacral vertebræ. The hæmal spines commence immediately behind the pelvic region. The number of vertebræ between the head and the caudal series is, as far as could be ascertained, correct. There may possibly be one additional vertebra present.

The restoration of the skull of *Sauropleura* (text-fig. 19) is based on the specimen of *Sauropleura marshii* (R. 2659). Jaekel (1909) has published a restoration of a Linton *Sauropleura* skull. There is no doubt, on the evidence afforded by

the British Museum material, that the orbits are placed very close together, and the interorbital distance is narrow, also that the external nares are elongate slits. In these two respects Jaekel's restoration of the skull is inaccurate.

The exact resemblance of the Nürschan species *Sauropleura distinctus* (Fritsch) to the Linton species of *Sauropleura* I hope to make clear in a later paper. The Nürschan species retains a larger supratemporal bone and somewhat larger limbs, and in these respects is the more primitive form.

Genus Ctenerpeton Cope, 1897.

Cope, 1897, Proc. Am. Phil. Soc. xxxvi. p. 83, pl. 3, fig. 1.

Ctenerpeton remex Cope.

Cope, 1897, Proc. Amer. Phil. Soc. (*Ctenerpeton alveolatum*).
Cope, 1875, Geol. Surv. Ohio, ii. (*Estocephalus remex* tails).

Material:—

R. 2548. Impression of ventral armour similar to that figured by Moodie (1916) on Pl. 23, fig. 2.

R. 2658. Impression of vertebral column, neural and hæmal spines smooth, with pectinate edges.

Measurements:—

Average length of scale, 8·78 mm.; average breadth of scale, 3·44 mm.

R. 2548 is a fragmentary portion of the ventral dermal armour of *Ctenerpeton remex*. It is, although larger, identical in appearance with the figure given by Moodie of Cope's type-specimen. This specimen, while it is fragmentary, is of interest, since it shows that each "angulated dermosseus rod" consists of a number of plates, or scales. The anterior posterior overlap margin of the scales bears an ornament of bosses as shown in Moodie's figure, while the lateral overlap margins are unornamented.

The vertebræ in this collection are much smaller than those of the type-specimen of *Ctenerpeton*. Both neural and hæmal spines of the vertebræ are expanded and fan-like, with slender bases. The free distal end of the spine bears a series of tiny spines. They are isolated, with no other remains associated with them.

Diceratosaurus brevirostris (Cope).

The suggestion made by Romer that the T-shaped cleithrum of *Batrachiderpeton lineatum* described by Professor D. M. S. Watson and the similar bones which occur in association with the skulls of *Keraterpeton galeani* and *Diceratosaurus brevirostris* are scapulæ cannot be upheld, as a cleithrum of this type is recorded by Douthitt (1917) associated with a scapula and a clavicle in *Diplocaulus*.

Order Adelospondyli Watson, 1929*.

Genus Cocytinus Cope, 1871.

Cope, 1871, Proc. Am. Phil. Soc. xii.

* This paper in the 'Palæontologia Hungarica' was set up in type in 1923 and bears that date. On the cover it is dated 1926. Some proof sheets may have been circulated in that year. In 1929 it reached certain libraries, but was not extensively distributed till 1930.—D. M. S. W.

COCYTINUS GYRINOIDES Cope.

Cope, 1871, Proc. Am. Phil. Soc. xii. p. 177.
Cope, 1874, Trans. Amer. Phil. Soc. p. 278.
Cope, 1875, Geol. Surv. Ohio, ii. p. 364, pl. 39, fig. 4.
Moodie, 1916, Coal Measures Amphibia of N. Amer. p. 68, figs. 16, 16 *a*.

Mologophis wheatleyi Cope.

Cope, 1874, Trans. Amer. Phil. Soc. xv. p. 263.
Cope, 1875, Geol. Surv. Ohio, ii. pp. 369–370, pl. 45, fig. 1.
Moodie, 1916, Coal Measures Amphibia of N. Amer. p. 149.

Material:—

R. 2663. Impression of length of vertebral column and associated ribs, showing no structure. No limbs present. Imperfect preservation due to covering of the bones with shale.

Total length, 10·5 mm.

R. 2544. Impression of entire animal. Limbs incomplete, and some caudal vertebræ missing. Skull represented by an impression of the cranial roof. Branchial arches and lower jaw also preserved (Pl. V. figs. 2, 3, 4; text-fig. 21).

Total length preserved, 11·5 cm.; length fore limb to hind limb, 10·27 cm.; breadth of table of skull, 6·4 cm.; length of humerus, 2 mm.; length of femur, 3 mm.; length of radius, 1·7 mm.

The second specimen of *Cocytinus gyrinoides* is very perfectly preserved and all details of structure are clearly shown. In general structure it resembles that of *Lysorophus*. The skull-roof is incomplete anteriorly (text-fig. 21, A). The nasals are two oblong rectangular bones; the anterior margins are absent. The frontals and parietals resemble the nasals in shape; and the series form a broad flat dorsal surface to the skull. Lying in an asymmetric position to one side of the medial parietal suture is the pineal foramen. The parietals are broad and extend laterally beyond the nasals, and it is into the anterior face of this lateral extension that the prefrontal fits.

The right tabular * is present, but does not extend to the mid-dorsal line of the skull. The medial sutures of the skull-roof are symmetrical, and the tabular is not displaced, so that, as in *Lysorophus*, the supraoccipital must have appeared on the dorsal skull-roof.

The cheek is represented by two bones. The prefrontal is bluntly triangular in shape, the long side of the triangle lying against the nasal and frontal bones, its posterior corner fitting into the anterior face of the lateral projection of the parietal. The prefrontal stretches down towards the margin of the jaw, and this marginal part is thickened. The posterior bone stretches from the table of the skull to the articular region of the lower jaw. In *Lysorophus* it takes part in the formation of the condyle and unquestionably must be, at least in part, the quadrato-jugal. In *Cocytinus* the articular end of this bone is rounded and fits into the depression which is the articular surface for the condyle on the lower jaw. If this bone, then, is the quadrato-jugal (=squamosal of *Lysorophus* (Sollas)), the small curved bone lying between the quadrato-jugal and the parietals is the squamosal bone (=supratemporal of *Lysorophus* (Sollas)).

Between the quadrato-jugal and prefrontal and in front of the prefrontal, indications of ossifications in the neural cranium are present. These impressions are very faint, and I found it impossible to find any very certain structure there.

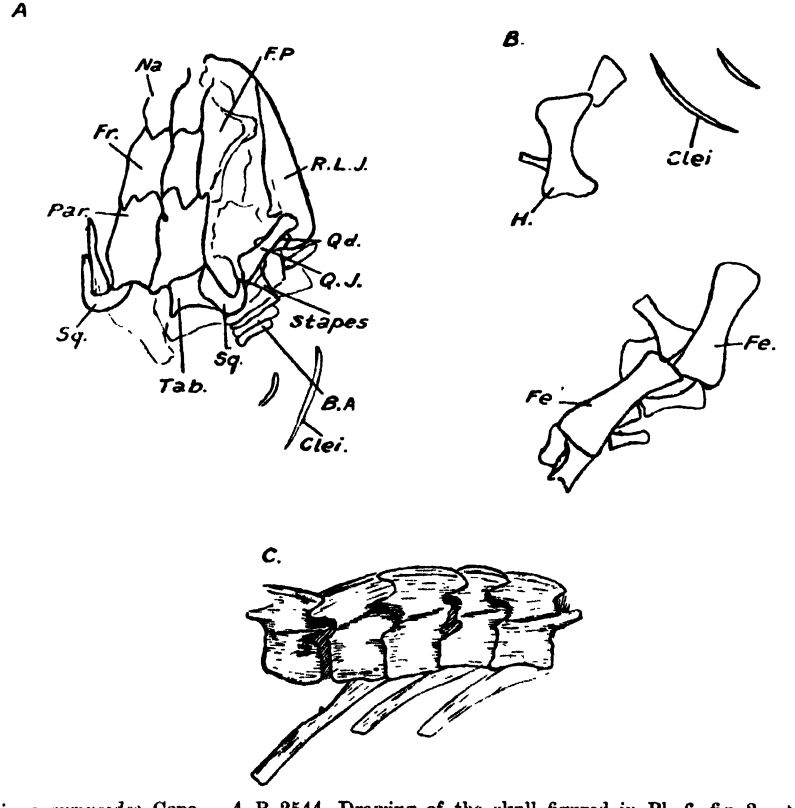
* There is no evidence of the correct homology of this bone. Professor Sollas has called the similar bone in *Lysorophus* the tabular, and I have used this name here. It may represent a tabular, a supra-temporal, or a dermo supraoccipital.

There is, lying internal to the squamosal and somewhat diagonally across it, a small bone which is almost sitting on the articular facet of the lower jaw, and this is the quadrate or quadrate and articular.

The lower jaw is characteristic in shape. It shows no sutures, and there are no teeth preserved. The ventral margin is straight, and the articulation of the quadrate is low down and near the ventral margin of the jaw.

Beneath the quadrato-jugal lies the stapes. It is a bone consisting of a basal

Text-figure 21.



Cocytinus gyrinoides Cope. *A*, R. 2544. Drawing of the skull figured in Pl 6, fig. 2 × 3·5 *B.A.*, Epibranchials. *B*, Right fore, × 6·5 and, hind limbs × 5·6. *C*, Connected series of vertebræ and ribs taken some distance in front of the sacral region; lateral view from the right side, Pl. VI. fig. 4. × 4.

plate and a pointed process directed backwards. Between the plate and the process there is a break.

The ornament consists of a few faint striæ and pits developed on the dermal bones.

The branchial arch skeleton is represented by four elements lying in close succession to one another immediately behind the skull. These are slightly curved bony rods, the ventral ends of which are slightly expanded. The first three are of the same size, but the fourth element is much smaller. They are presumably the

epibranchial elements of the four branchial arches. Of the remaining elements of the branchial arches, and of the hyoid bones, there are no traces, with the exception of an imperfect impression of one other bone, belonging to the branchial arch skeleton, below the epibranchial series.

The vertebral column of *Cocytinus gyrinoides* is also complete. In all eighty-one vertebræ are present. There are four vertebræ anterior to the level of the shoulder-girdle, but the structure in this region is incompletely shown. The two vertebræ immediately in front of the shoulder-girdle carry small and slender ribs.

The dorsal series of vertebræ lying between the shoulder-girdle and the pelvic girdle consists of some sixty-three vertebræ. These all carry ribs except the last four (? three) presacral vertebræ. The ventral margins of the centra are slightly concave, the breadth and height are approximately the same. That the centra are hollow is indicated by the depression on their lateral surface. A side view of the neural arch is shown in Pl. VI. fig. 4 & text-fig. 21, C. The pre-zygapophyses are well developed with a flattened upper face with which the post-zygapophyses articulate. The vertebræ in the specimen are shown in natural articulation, and where this is so the neural arch extends anteriorly over the post-zygapophyses of the preceding vertebræ. The post-zygapophyses are stout and project somewhat laterally from the vertebræ. In some of the vertebræ inter-vertebral foramen are shown. The transverse processes are carried below the pre-zygapophyses and near the anterior face of the vertebræ. I could detect no facet on the centra for the capitum of the rib.

The structure of the remaining eleven vertebræ is not distinctly shown; they resemble the dorsal vertebræ in structure. No ribs are present, and there appears to be no differentiated sacral vertebræ.

Ribs are present on the first sixty-two (? sixty-three) dorsal vertebræ, and on the two posterior cervical vertebræ. They do not differ greatly in size, the cervical ribs and the last of the dorsal series being smaller and more slender. They are slightly curved with the ventral end expanded. The proximal end appears broad, but it is not clear whether they are single or double-headed.

The shoulder girdle of *Cocytinus* is loosely connected with the ribs, as both shoulder-girdle and fore limb are displaced (text fig. 21, B). The girdle is represented by two curved bony splints which are presumably clavicles. Above the head of the humerus lies a small bone, which may represent the scapula. It is flat, and there is no trace of any depression on it. The humerus is represented by a flat bony plate, of which the anterior margin is more concave than the posterior one. The remaining bones of the fore limb have not been preserved, except for a small metacarpal bone lying on the posterior margin of the humerus.

The hind limb is also displaced. Both femora are present, and situated at the distal end of one femur lie the proximal ends of tibia and fibula. One or two metatarsals are present. Both the proximal and the distal ends of the femur are expanded. These expansions are flat, but the intervening part is strongly rounded. Behind the femur lies a bone which appears to have one end broader than the head of either tibia or fibula, and which is possibly a pelvic girdle bone.

It is impossible to ascertain the structure of the sacral vertebræ. They appear to resemble exactly the dorsal vertebræ in structure and proportion but carry no ribs.

The fore limb is slender and delicate when compared with the more massive hind limbs. Although more developed, both fore and hind limbs are absurdly small and must have proved ineffective structures.

Systematic Position of Cocytinus.

Cocytinus gyrinoides is at once distinguished from the other species of this fauna by the well-ossified vertebral column, and a skull in which the cheek-bones are largely unossified, associated with the presence of a hyobranchial apparatus. All

these suggest immediately its relationship to *Lysorophus*, a suggestion which has already been put forward by Professor D. M. S. Watson.

If the skull be compared with that of *Lysorophus* the similarity even in detail is striking. The rectangular nasals, frontals, and parietals, the curious sigmoid squamosal, the articulation of the prefrontal with parietal, nasal, and frontal, and the absence of all the cheek-bones except the prefrontal and quadrato-jugal, all point to a minute similarity in structure between the two forms. The lower jaw is identical in shape, and in the fact that the hinder end of the dentary rises as a coronoid process high above the articular surface of the jaw. In both the branchial arch skeleton, four arches in *Cocytinus* (three with remnants of a fourth in *Lysorophus*), and the hyoid bones (shown in Cope's specimens of *Cocytinus gyrinoides*) are similar. Further, the vertebral column in *Cocytinus* resembles that of *Lysorophus*, except for the anterior extension of the neural arch elements in *Cocytinus*. Fore and hind limbs are present, and in both the hind limb is the larger structure.

A statement of the existing differences will make the exact resemblance of the two forms clearer. These are:—

1. The presence of a minute pineal foramen in *Cocytinus gyrinoides*, which is asymmetric in position. There is no pineal foramen in *Lysorophus*.
2. The presence of a fourth well-ossified branchial arch in *Cocytinus*.
3. The extension of the neural arch of the vertebræ more anteriorly than in *Lysorophus*.

The pattern of the skull (as far as this is shown by *Cocytinus*), the structure of the vertebræ (except for a minor difference), the limbs and the character of the hyobranchial apparatus, then, are identical in both forms.

Cocytinus gyrinoides, therefore, is very closely allied to *Lysorophus* and belongs to the order Adelospondyli. There is no evidence in this specimen that there is a separate neural arch and centrum ossification, as the vertebræ are preserved in an undisturbed condition.

The structure of *Cocytinus gyrinoides*, while of no value as a stage in the derivation of the *Lysorophus* skull from a type like that of *Adelogyrinus simorhynchus* or *Dolichoparcias dejectus* (in which reduction of the cranial bones has already commenced), is of great interest. *Cocytinus* occurs in the Middle Coal Measures at Linton, and is therefore intermediate in age between *Adelogyrinus*, etc., from the lower Carboniferous of Scotland, and *Lysorophus*, which is found in beds of extreme U. Carb. age in Texas. It is remarkable that the very specialised type of skull structure exemplified in the *Cocytinus Lysorophus* group occurred as early as the Middle Coal Measures and persisted unchanged to the top of the Carboniferous period.

Lower jaw of an Adelospondyl.

There is present in the British Museum collection a specimen (R. 2667) on which the anterior part of a lower jaw is present. The jaw is slender with a flat ventral margin, and a short tooth row with very large erect teeth of much the same size. This jaw resembles, so far as preserved, that of a *Cocytinus* or *Lysorophus* form. The occurrence is of interest, as it suggests the presence of a comparatively large Adelospondylous form amongst the Linton fauna.

Genus PLEUROPTYX, Cope, 1875.

Cope, 1875, Geol. Surv. Ohio, ii. p. 370.

PLEUROPTYX CLAVATUS Cope.

Cope, 1875, Geol. Surv. Ohio, ii. p. 370, pl. 42, fig. 1; pl. 44, fig. 2.

Material:—

R. 2670. Impression of ribs and vertebræ (Pl. VI. fig. 5).

Measurements:—

Length of centrum, 7·2 mm.; length of neural spine, 8·5 mm.; depth of vertebræ, 17·0 mm.; length of arc of rib, 27·0 mm.; width of ala, 5·0 mm.; width of rib at extremity, 2·5 mm.

Pleuroptyx clavatus is represented by an impression of several vertebræ and the associated ribs. It is identical with the specimen figured by Cope (Geol. Surv. Ohio., pl. 44, fig. 2) but is smaller.

The vertebræ are well shown. The centra are massive, and one which shows the ventral surface displays a ventral medial rib, on either side of which the surface is deeply concave. The neural arches at one end of the specimen are separate from their centra. These carry, somewhat anteriorly, broad transverse processes. The zygapophyses are well developed. The neural arches form a low medial arch projecting anteriorly above the pre-zygapophyses.

The ribs are stout and curved, but the proximal end is not shown. The posterior ala is a thin flat laminar expansion narrowing towards the distal end of the rib shaft.

The structure of the rib is paralleled in no other known form, and the vertebræ have a separate neural arch and centrum ossification. *Pleuroptyx clavatus* is therefore assigned on the structure of its vertebral column to the order Adelospondyli. In connection with the systematic position of Pleuroptyx it is of interest to note that a larger Adelospondylous form than *Cocytinus* occurs in the Linton fauna, as exemplified by an isolated lower jaw.

The collection of material from Linton includes also the following specimens:—

Order Labyrinthodontia.

Orthosaurus sp.

P. 2675 (B.M. 64). Fragment of the cheek of an Orthosaurid skull which cannot be distinguished from the English specimens of *Orthosaurus*. This skull and that of the Labyrinthodont (R. 2675) are much the largest forms present in this fauna.

Labyrinthodont.

R. 2675 (B.M. 63). Fragment of a large skull, too incomplete to make identification possible. Probably an Embolomerous form.

The Structure of the Vertebral Column in the Linton Phyllospondyli.

There occurs in association with the skull of *Erpetosaurus radiatus* a number of scattered isolated somewhat triangular plates. Similar elements are associated with the skull of *Stegops divaricata*, but in this case two neural arch elements, comparable in structure with those of a Phyllospondyl such as *Branchiosaurus*, are also present. The evidence that these triangular plates represent vertebral elements was afforded by a single specimen both slab and counterpart (R. 2664), between which a section of the dermal armour of a scaled Amphibian was preserved. In this specimen the ventral scales remain for the most part undisturbed, so that the complete ventral armour of the animal is shown. The individual scales (in length 4 mm. and 1·5 mm. broad) are elongate, parallel sided with rounded ends, and smooth on both inner and outer sides. Across the inner surface of these ventral scales there lies a single row of triangular plates (length 4 mm., height 8 mm.) (Pl. IV. fig. 2) identical with those of *Erpetosaurus radiatus* and *Stegops divaricata*. The structure of these plates, as shown, admits of no intelligent

interpretation, but there can be no doubt that these elements form an integral part of the vertebral column. On the free margin of the ventral armour, and superimposed on the vertebral elements and the inner surface of the ventral scales, lie numerous fragile oval scales (length 2·5 mm.) which show a delicate ornament of concentric rings, and in some cases faint radial striæ. They are not comparable to fish scales, are too numerous for their presence here to be accidental, and can only represent dermal dorsal scales. The point is an important one, as it is consistent with the occurrence of two types of scales in association with many of the Linton Phyllospondylian skulls, and in addition brings the Linton fauna into agreement with the Nürschan Amphibia, in which a similar form of scaling occurs.

The type of vertebra which occurs in these Linton species is clearly only comparable, amongst the Palæozoic Amphibia, to that of a Phyllospondyl.

In the Phyllospondyli the structure of the vertebral columns is known for the most part in later members of the order such as in the Branchiosaurs, etc. Here the vertebræ consist of ossified neural arch elements with no trace of centra, and this type of vertebral column is in keeping with the general reduction of ossification of the skeleton. In *Eugyrinus wildii* neural arches are known and no centra appear to be present.

An interpretation of the structure of the vertebral column in *Stegops divaricata* was suggested to me by Professor D. M. S. Watson. In a specimen of *Limnerpeton laticeps*, figured by Fritsch (Fauna der Perm. formations Böhmens, Bd. i. pl. 36, fig. 1), there occurs in the vertebral column of a single individual anterior vertebræ with well-developed neural arches, succeeded by more posterior vertebræ in which the neural arches are represented by somewhat triangular plates. This, then, is the explanation of the structure of the vertebral column of the Linton Phyllospondyli, and of the association of normal neural arch elements with triangular plates such as occur in *Stegops divaricata*. In *Erpetosaurus radiatus*, the only other species in which the vertebræ column is known, it is formed for a considerable distance posterior to the interclavicular region by these triangular plates.

The ossification of the vertebral column, then, in these Middle Coal Measures forms is as incomplete as in Lower Permian species. That this is so, is supported by the condition of the vertebral column in *Eugyrinus wildii*.

The structure of the vertebral column in the Linton species is consistent with what is known of the palate and the skull.

The Linton Phyllospondyli.

The cannel coal bed at Linton is the earliest known deposit from which Phyllosopondyli have been recorded, with the exception of *Eugyrinus wildii* from the L. Coal Measures of Lancashire. The morphology of the Linton species is, therefore, of the greatest importance from its bearing on the evolution of the Phyllospondyli.

The discussion of their morphology, which has been given, can leave no doubt that they form a series of related forms, with a common basis of skull structure, in which all the evidence is consistent with their systematic position in the Phyllospondyli. The most complete confirmation of this, as Romer has pointed out, is the close agreement of the skulls of *Pelion lyelli* and *Eugyrinus wildii*. *Pelion lyelli* retains an intertemporal bone in the skull-roof. This bone is already lost in *Eugyrinus wildii*, and is present in no other Linton species except *Branchiosauravus*. On the other hand, the skull of *Erpetosaurus*, while retaining many primitive characters such as large basioccipital, single basioccipital condyle into which the exoccipitals enter, small parasphenoid, and narrow interpterygoid vacuities, presents a palate of a primitive Branchiosaur type. It is therefore quite clear that this series of Linton forms can be identified through *Pelion lyelli* with

Eugyrinus wildii, while on the other hand, *Erpetosaurus* exhibits many features which are characteristic of the Carboniferous and early Permian Labyrinthodonts. While this so, the more advanced members of this fauna, such as *Stegops*, are Branchiosaur like.

The individual skulls present combinations of advanced and primitive characters, and it is possible to form, within the Linton species, a morphological series for any one character of skull structure, of which character the final result is expressed in the Branchiosaurs. The morphological changes which the series presents are these:—

1. The skull becomes dorso-ventrally flattened, e. g., *Erpetosaurus* and *Colosteus*, *Stegops*, *Branchiosaurus*.

2. The intertemporal bone is already lost in the Linton species with the exception of the species *Pelion lyelli* and *Branchiosaurus*.

3. The ectopterygoid, which is present in all the Linton species, is absent in the Branchiosaurs. Correlated with this is the extension of the subtemporal fossa anteriorly. A slight extension of the subtemporal fossa anteriorly is seen in *Erpetosaurus lævis*.

4. The interpterygoid vacuities increase in size—cf. *Erpetosaurus*, *Stegops*, *Branchiosaurus*.

5. The movable articulation between the pterygoid and the basipterygoid processes of the parasphenoid is replaced by a sutural union—cf. *Erpetosaurus* and *Pelion lyelli*, *Stegops* and *Platyrhinops*.

6. The posterior plate of the parasphenoid becomes expanded—cf. *Erpetosaurus*, *Steyops*, *Pelion*.

7. The length of the quadrate ramus of the pterygoid becomes reduced—cf. *Platyrhinops*, *Pelion*, *Branchiosaurus*.

The previous considerations can lead only to the following conclusions:—

That

1. The more primitive Linton species, such as *Erpetosaurus*, share certain features in common with the skulls of Carboniferous and early Permian Labyrinthodonts. These features, which disappear completely in later members of both orders, are direct inheritances from a common ancestor.

2. The Linton species are morphologically the potential ancestors of later Phyllospondyli, such as the Branchiosaurs, and not aberrant forms. In every character of skull structure they are the more primitive.

3. The series of differences which separate them from the Branchiosaurs are identical with the series of changes which take place with time in the order of the Labyrinthodontia.

4. This series of changes take place in the Phyllospondyli at a much earlier period than in the Labyrinthodonts. *Erpetosaurus radiatus* presents a similar morphological evolutionary stage to that of *Eryops*—a Rachitimous Labyrinthodont from the L. Permian.

The skull of *Erpetosaurus radiatus*, in which many of the characteristics of the Carboniferous or early Permian Labyrinthodont skulls are present, does in part solve the question of the relationship of the Phyllospondyli and the Labyrinthodontia. It is evident that the intervening morphological stages must be sought at a much earlier geological period.

From the Linton fauna there is gained some idea of the diversity of structure which the Phyllospondyli present as early as the M. Coal Measures period. It is of interest that these, some of the earliest known members of this group, already attain a stage of morphological specialisation, which is reached in the Labyrinthodontia only at a much later geological period. The Linton Phyllospondyli are therefore still further characterised by the precocious development of those evolutionary changes which take place in the Palæozoic orders of Amphibia.

Geographical Distribution.

It has already been pointed out by Romer that remnants of similar faunas to that of Linton are preserved at Jarrow (Ireland) and Nürschan, and that the later Permo-carboniferous faunas of America show little relation to these. He has included in his paper a summary of the inter-relation of these faunas.

On the evidence afforded by the Linton fauna, comparisons with other species, unless there is complete evidence of their systematic position, is unsatisfactory. There remains little to note, but I should like to emphasise the widespread distribution of Ophiderpeton. Almost identical species of this long-bodied legless Amphibian occur at Nürschan, Linton, Jarrow (Ireland), and Newsham (England). Species of Sauropleura are present both at Nürschan and Linton, and observations on the Nürschan species *Sauropleura distinctus* which I hope to publish will make clear the exact resemblance of the two forms. *Sauropleura distinctus*, in the retention of a larger supratemporal bone and somewhat larger limbs, is the more primitive.

Acanthostoma vorax is undoubtedly a Phyllospondyl, and in many respects closely allied to *Stegops divaricata*. There is no evidence that *Dasyceps*, *Zatrachys*, and *Platyhistrix* belong to this group.

It is possible that the small skull *Tersomius texensis* Cope from Texas is a Phyllospondyl.

A Bibliography of the fossil Amphibia is included in :—

Moodie, R. L. 1916. The Coal Measures Amphibia of North America. Publ. Carnegie Inst. Wash. no. 238.

Hay, O. P. 1902. Bibliography and Catalogue of the Fossil Vertebrata of North America.

——— 1929. Second Bibliography and Catalogue of the Fossil Vertebrata of North America. Publ. Carnegie Inst. Wash. no. 390, i.

Romer, A. S. 1930. The Pennsylvanian Tetrapods of Linton, Ohio. Bull. Amer. Mus. Nat. Hist. lix. pp. 77–147.

List of Works cited.

Broom, R. 1913. Studies on the Permian Temnospondylous Stegocephalians of N. America. Bull. Amer. Mus. Nat. Hist. xxxii, pp. 563–595.

Bulman, O. M. B., & Wittard, W. F. 1926. On Branchiosaurus and Allied Genera (Amphibia). Proc. Zool. Soc. pp. 533–579, pls. i.–iv.

Case, E. C. 1915. The Permo-carboniferous Red Beds of North America and their Vertebrate Fauna. Carnegie Inst. Wash.

——— 1926. Environment of Tetrapod Life in the later Palæozoic of Regions other than North America. Publ. Carnegie Inst. no. 375.

Cope, E. D. 1868. Synopsis of the Extinct Batrachia of North America. Proc. Acad. Nat. Sci. Philad. pp. 208–221.

——— 1869. Synopsis of the Extinct Batrachia, Reptilia, and Aves of North America. Trans. Amer. Phil. Soc. pp. i–viii, 1–252, pls. i.–xiv.

——— 1871. Supplement to the Synopsis of the Extinct Batrachia and Reptilia of North America. Proc. Amer. Philos. Soc. pp. 41–52.

——— 1874. Supplement to the Extinct Batrachia and Reptilia of North America—I. Catalogue of the Air-breathing Vertebrates from the Coal Measures of Linton, Ohio Trans. Amer. Philos. Soc. xv. pp. 261–278.

——— 1875. Synopsis of the Extinct Batrachia from the Coal Measures : Report of the Geological Survey of Ohio. Palæontology, ii. pp. 350–411, pls. xxvi–xlv.

——— 1885. Second Continuation of Researches among the Batrachia of the Coal Measures of Ohio. Proc. Amer. Philos. Soc. xxii. p. 406.

——— 1897. On New Palæozoic Vertebrata from Illinois, Ohio, and Pennsylvania. Proc. Amer. Philos. Soc. xxxvi. pp. 71 90.

Douthitt, H. 1917. The Structure and Relationships of Diplocaulus. Contrib. Walker Museum, ii. no. 1, pp. 3–41.

FRITSCH, A. 1899–1901. Fauna der Gaskohle und der Kalkstein der Permformation Böhmens, Bd. 4.

HANCOCK & ATTHEY, T. H. 1868. Ann. & Mag. Nat. Hist. i. pp. 276–277.

HUENE, F. VON. 1909. Neubischreibung des Permian Stegocephalian *Dasyceps bricklandi* (Lloyd) aus Kenilworth. Geol. u. Palæont. Abhandl. N. F. Bd. 8 (der ganzen Reihe, Bd. xii. ss. 325–338, Taf. 44, 45.

JACKEL, O. 1909. Ueber die Klassen der Tetrapoden. Zoologischen Anzeiger, xxxiv. pp. 204–210, fig. xiii.

MOODIE, R. L. 1909. New or little-known Forms of Carboniferous Amphibia in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. xxvi. pp. 347–351, pls. lviii.–lxv.

——— 1909. Carboniferous Air-breathing Vertebrates of the United States National Museum. Proc. U.S. Nat. Mus. xxxvii. pp. 11–28, pls. iv.–x.

——— 1909. A Contribution to a Monograph of the Extinct Amphibia of North America. New Forms from the Carboniferous. Jour. Geol. xvii. pp. 38–82, 24 text-figs.

——— 1914. A List of the described species of fossil Amphibia. Kansas Univ. Sci. Bull. ix. pp. 13–28.

SOLLAS, W. J. 1920. On the Structure of *Lysorophus* as exposed by Serial Sections. Phil. Trans. B ccix. pp. 481–527.

WATSON. D. M. S. 1913. *Batrachiderpeton lineatum* Hancock & Atthey, a Coal Measures Stegocephalian. Proc. Zool Soc. London, pp. 949–962, pls. xcvi.–xcvii.

——— 1917. A Sketch Classification of the Prejurassic Tetrapod Vertebrates. Proc. Zool. Soc. London.

——— 1919. Structure, Evolution, and Origin of the Amphibia, the orders Rachitomi and Stereospondyli. Phil Trans. B. ccix.

——— 1921. On *Eugyrinus wildii*, a Branchiosaur from the Lancashire Coal Measures. Geol. Mag. lviii. pp. 70–74.

——— 1925. Evolution and Origin of the Amphibia. Phil. Trans. B. ccxiv.

——— 1929 The Carboniferous Amphibia of Scotland. Palæontologia Hungarica, i.

WILLISTON, S. W. 1911. American Permian Vertebrates. Chicago.

WYMAN, J. 1858. On some Remains of Batrachian Reptiles discovered in the Coal Formation of Ohio. Amer. Journ. Sci. (ii.) xxv. pp. 158–164.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Erpetosaurus radiatus* (Cope). R. 2670. Palate. × 1·36.*

2. *Erpetosaurus radiatus* (Cope). P. 2672. Dorsal surface of the skull. × 0·95. Text-fig. 2.

3. *Erpetosaurus lævis* (Moodie). R. 2662. Ventral surface of the skull. × 1·54. Text-fig. 4.

PLATE II.

Fig. 1. *Colosteus scutellatus* (Newberry). R. 2547. Lateral aspect of the skull. × 0·74. Text-fig. 6.

2. *Stegops divaricata* (Cope). R. 2546. Ventral surface of the skull. × 1·3. Text-fig. 9.

3. *Stegops divaricata* (Cope). R. 2668. Dorsal surface of the skull. × 1·03. Text-fig. 8.

PLATE III.

Fig. 1. *Platyrhinops mordax* (Cope) (gen. n.). R. 2670. Dorsal surface of the skull. × 1·16. Text-fig. 11.

2. *Platyrhinops mordax* (Cope) (gen. n.). R. 2670. Ventral aspect of the palate. × 1·08. Text-fig. 12.

3. *Mytaras macrognathus*, gen. et sp. n. R. 2657. Ventral aspect of the skull. × 1·19. Text-fig. 14.

* Except where otherwise stated, all photographs are of plasticene or dental wax squeezes.

Plate IV.

Fig. 1. *Pelion lyelli* Wyman. P. 2674. Ventral aspect of the skull. × 2·86. Text-fig. 15.
2. Vertebral column and dermal armour of a Phyllospondyl. × 1·41. R. 2664.

Plate V.

Fig. 1. *Ophiderpeton amphiuminus* (Cope). R. 2657. Lateral aspect of the skull. × 1·39. Text-fig. 17 B.
2. *Ophiderpeton amphiuminus* (Cope). P. 2673. Skull. × 1·94. Text-fig. 17 A.
3. *Ophiderpeton amphiuminus* (Cope). P. 2673 Vertebræ and ribs, × 1·81.

Plate VI.

Fig. 1. *Sauropleura marshii* (Cope). R. 2659. Dorsal surface of the skull.
2. *Cocytinus gyrinoides* Cope. R. 2544. × 1·06.
3. *Cocytinus gyrinoides* Cope. R. 2544. Enlarged anterior part of specimen in pl. 6, fig. 2. × 2·33.
4. *Cocytinus gyrinoides* Cope. R. 2544. Enlarged sacral and presacral region of the specimen, pl. 6, fig. 2. × 3·0.
5. *Pleuroptyx clavatus* Cope. R. 2676. Vertebral column. × 1·42.

The following abbreviations have been used in the text-figures:—

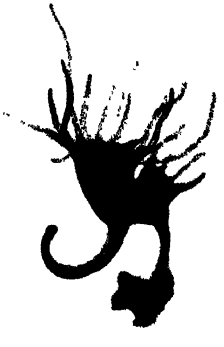
Ang. Angular.
B.Oc. Basioccipital.
C.F. Carotid foramen.
Cl. Clavicle.
Clei. Cleithrum.
Den. Dentary.
Ec.Pt. Ectopterygoid or transverse bone.
Ex.Oc. Exoccipital.
Ext.Nar. External nares.
F.O. Fenestra ovalis.
F.P. Prefrontal.
Fe. Femur.
Fr. Frontal.
H. Humerus.
I.Cl. Interclavicle.
Il. Ilium.
Int.nar. Internal nares.
Ju. Jugal.
L.L.J. Left lower jaw.
La. Lachrymal.
Mx. Maxilla.
Na. Nasal.
Orb. Orbit.
P.B.Pt. Basipterygoid processes of parasphenoid.
P.F. Post-frontal.
P.Mx. Premaxilla.
P.O. Postorbital.
P.R.Pt. Palatal ramus of pterygoid.
P.V. Prevomer.
Pal. Palatine.
Par. Parietal.
Par.Oc. Paroccipital process.
Pro.Ot. Pro-otic.
Psp. Parasphenoid.
Pt. Pterygoid.
PT.SP. Post splenial.
Q.J. Quadrato-jugal.
Q.R.Pt. Quadrate ramus of pterygoid.
Qd. Quadrate.
RA. Radius.
S.Ang. Surangular.
S.O.P. Supraorbital plates.
S.T. Supratemporal.
S.T.S. Supratemporal spine.
Sc. Scapula.
Sp. Splenial.
Sq. Squamosal.
Tab. Tabular.
Ul. Ulna.
XII. Foramen for hypoglossal nerve.
V.M.R. Ventral medial ridge.



1.



2.



3.



4.

John Bale, Sons & Danielsson, Ltd. London.

ON THE BUDDING OF A SCYPHISTOMA.

40. On the Budding of a Scyphistoma.

By RACHEL M. RENTON, F.Z.S.

[Received May 16, 1930: Read October 21, 1930.]

(Plate I.*; Text-figure 1.)

The Scyphistoma was first found unattached and floating in a tank in a small Marine Aquarium at University College, London, in February 1929, the sea-water for the tanks having been obtained from Plymouth some six months before. Since then it has made its appearance in four different tanks, growing on the stones and shells often in considerable numbers.

The normal individual is very small and of a semi transparent white, measuring just over 1 mm. in height, about ½ mm. across the polyp, and the stalk usually about ½ mm. when not extended; the length of the tentacles varies very considerably, being sometimes when fully extended as much as 1 mm. or occasionally even more than this. The polyp is bell-shaped, and the tentacles number either 16 or 20, rarely anything between.

In the bud one tentacle usually makes its appearance, followed rapidly by three more, then another set of four, and by the time the bud has separated there are at least twelve or even sixteen. Up to the present I have never observed budding taking place in a polyp with fewer than sixteen tentacles. The stalk is normally rather short and thick, but it can be extended to twice or three times its ordinary length, becoming very thin and fine.

The mouth, which lies in the middle of a flat disc, is four cornered, with a thickened rim on each of the four sides; being very elastic it can be opened to the extreme edge of the disc; sometimes two sides will stretch and open, while the other two remain still. The opening and closing take place by means of four muscle bands, one at each corner of the mouth, which extends radially to the margin of the disc.

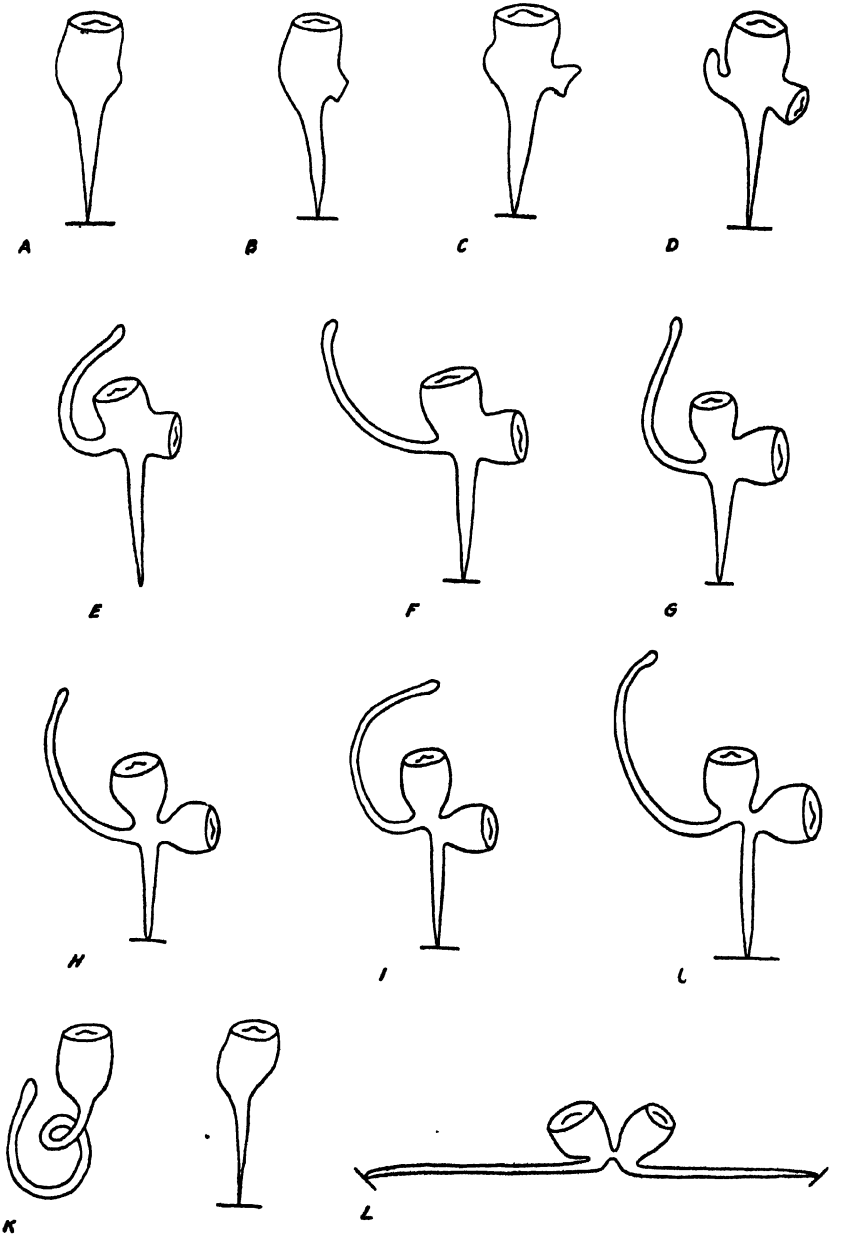
The first specimens were put into a finger-bowl containing water from the tank in which they were found, and budding began almost at once. Between then and the present date, February 1930, a very large number of individuals have been kept under observation in finger-bowls, and at the same time small stones on which the Scyphistoma were growing have been closely studied, and in every case the method of budding has followed exactly the same course.

The chief point of interest in this process lies in the fact that the new polyp remains fixed to the parent stalk, while the parent polyp grows a new stalk, then separates from the bud and finally becomes attached by the newly-formed stalk, either close to the new polyp or some distance away. Occasionally the new stalk fixes itself to the finger-bowl or stone before the polyps have become completely separated (text-fig. 1, L).

A series of diagrammatic drawings (with the tentacles omitted) illustrate this method of budding and growth of stalk. The bud appears as a small bulge at the side of the polyp (text-fig. 1, A) and grows quickly outwards and slightly downwards (text-fig. 1, B). About the second day the stalk appears as a small outgrowth on the opposite side of the polyp (text-fig. 1, C) and extends outwards and upwards (text-fig. 1, D, E, F). About the fourth day the tentacles appear, although in some cases one has begun to show earlier than this. As the new polyp

* For explanation of the Plate, see p. 896.

Text-figure 1.



Diagrammatic drawings of a Scyphistoma (with tentacles omitted) illustrating the process of budding.

increases in size a constriction begins to be seen between it and the parent (text-fig. 1, G, H), and this soon becomes well marked above and below.

At the stage reached in text-fig. 1, I, J, this process has continued to such an extent that the connection between the two polyps has become very slender. Finally about the eighth or ninth day (the time varies) the two polyps are completely separated (text-fig. 1. K), the new individual remaining fixed on the parent stalk, and the parent polyp attaching itself by the new stalk to the glass or stone. After an interval of a few days both polyps begin to bud anew. The only variation that has occurred has been in the relative sizes of the bud and new stalk; in a few cases the bud being already fairly large when the stalk first made its appearance, though it is more usual for the stalk to appear immediately after the bud and grow rapidly. During growth the new stalk is very active, stretching out to a great length and then contracting suddenly, after coiling itself round the polyp. Even when fixed it remains very sensitive, and at a touch or sudden slight movement of the finger-bowl will contract violently drawing the polyp down.

When not engaged in budding the Scyphistoma spreads its tentacles out and by means of the flexible stalk bends itself in all directions in its search for food, which seems to consist for the most part of Protozoa which are caught on the tips of the tentacle, the latter being then thrown into the mouth and slowly withdrawn. Sometimes several tentacles are cast in the mouth at once.

It may be worth noting that I have tried feeding the Scyphistoma on a nutritive fluid made from raw meat or fish, and have observed the tentacles catching minute portions of the food, but owing to the habit of the animal of suddenly contracting and remaining in this position for a considerable time at the slightest disturbance of the water, they are not very easy to feed artificially.

Perez has described two types of budding, one of which takes place on a stolon growing out from the side of the parent polyp; his illustrations of this method show the latter tapering slightly towards the base, where it is fixed by a short thick stalk, quite unlike the noticeably differentiated stalk and polyp of the type I have described. The bud continues to grow on the stolon, which becomes very thin, and as the bud fixes itself the connecting stolon breaks and the young Scyphistoma becomes independent.

In Perez's other account the bud grows out directly from the lateral surface of the polyp and has no connection with the stolon; in this respect the budding is of the same type as in the specimen I have described.

The important point of difference occurs in the formation of the new stalk; in Perez's Scyphistoma the bud grows a stalk and fixes itself by this, while in the other case, of which I have given a full account above, the bud remains fixed to the parent stalk, and the parent takes the new stalk and fixes itself by this. In Hérouard's account the budding is of the former type, in which the bud grows from the stolon, and this method is followed in some other specimens which I have had under observation in the Aquarium at University College.

In conclusion, I should like to express my thanks to Professor D. M. S. Watson, F.R.S., and also to Captain A. K. Totton, of the British Museum (Natural History), for their kind assistance and advice; to Mr. W. H. T. Tams, of the British Museum (Natural History), I am indebted for the photographs of the Scyphistoma.

Bibliography.

1. Perez, Ch. Observations sur la Multiplication d'un Scyphistoma. Bull. Biol. Fr. et Belg. lvi. 1922, pp. 244–274.

2. ——— Un élevage de Scyphistoma de Cyanea. Bull. Biol. Fr. et Belg. liv. 1920-21, pp. 168–178.

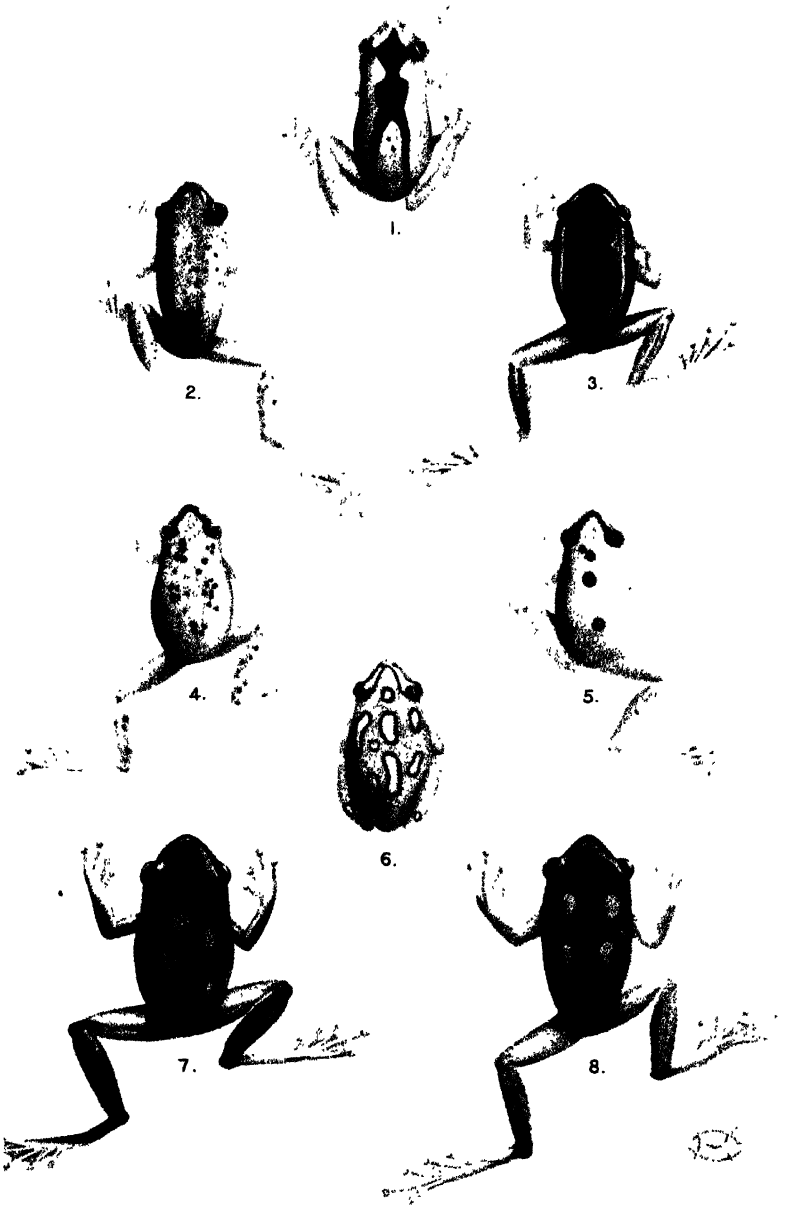
3. ——— Processus de Multiplication par bourgeonnement chez un Scyphistome. Bull. Soc. Zool. France, xlv. 1920.

4. Hérouard, E. Existence de Statoblasts chez le Scyphistome. C. R. Acad. Sc. Paris, clxv. 1907.
5. ——— Sur les Cycles évolutifs d'un Scyphistome. *Ibid.* t. cxlviii. 1909.
6. ——— Sur le mode de fixation au sol des Scyphistomes par des tonofibrilles. Bull. Soc. Zool. France, xxxvi. 1911.
7. Hadzi, J. Ueber die Podozystender Scyphopolypen. Biol. Centralblatt, xxxii. 1912.
8. Ballowitz, E. Ueber Hypomerie und Hypermerie bei *Aurelia aurita*. Lam. Arch. f. Entwichl. Mech. viii. 1899.
9. Agassiz, L. Contributions to the Natural History of the United States of America. T. iii. Boston, 1860.

EXPLANATION OF THE PLATE.

Fig. 1. Scyphistoma, with tentacles extended.
2. Scyphistoma, with bud.
3. Showing bud fixed to piece of stone.
4. Showing parent with tentacles fully extended.

(Untouched photographs of living specimens at a magnification of about 30 diameters by Mr. W. H. T. Tams.)



FROGS FROM PORTUGUESE EAST AFRICA.

41. A Collection of Frogs from Portuguese East Africa.

By H. W. Parker, B.A.*

(Submitted for publication by permission of the Trustees of the British Museum.)

[Received July 3, 1930: Read November 4, 1930.]

(Plate I.†)

During his expedition to the mouth of the Zambesi on behalf of the Zoological Society ‡, Mr. H. B. Cott made a large collection of preserved, as well as living, animals, and the author is indebted to him for the opportunity of studying the frogs of this collection. It has been considered advisable to give a complete list of the species, since, in addition to new species, others have not previously been recorded from this particular region. The localities have already been adequately described §, and all the specimens mentioned below have been presented to the British Museum.

Ranidæ.

1. Rana adspersa (Tschudi).

2 Caia; 3 Mutarara.

2. Rana delalandii (Tschudi).

1, 50 miles N. of Mutarara.

3. Rana galamensis Dum. & Bibr.

6 Fambani River.

4. Rana angolensis Bocage.

3 Amatongas.

One specimen, though measuring 34 mm. from snout to vent, has a persistent larval tail 6 mm. long; other newly-metamorphosed specimens of this species measure only 21 mm., the tail being then completely absorbed.

5. Rana nutti Boulenger.

1 Amatongas.

Nieden ‖ has considered this species a synonym of the preceding, but Barbour and Loveridge ¶ have maintained that *angolensis* is distinguishable by its longer snout. Comparison of several specimens supports the latter contention, and the differences noted may be expressed thus:—

A. Snout 1¾ the diameter of the eye; nostril nearer the eye than the end of the snout; tympanum ⅔ the diameter of the eye; length of the foot contained 1¾ in the distance from snout to vent ... *R. angolensis.*

B. Snout 1½ the diameter of the eye; nostril midway between the eye and the end of the snout; tympanum ½ the diameter of the eye; length of the foot contained 1⅔ in the distance from snout to vent *R. nutti.*

* Communicated by H. B. Cott, F.Z.S.

† For explanation of the Plate, see p. 905.

‡ Cott, Proc. Zool. Soc. London, 1928 (4), pp. 923–61.

§ Cott, *tom. cit.*

‖ Mitt. Mus. Berlin, vii. 1915, p. 352.

¶ Mem. Mus. Comp. Zool. I. (2) 1928, p. 195.

6. RANA ANSORGII Boulenger.

10 Amatongas.

Although this species has hitherto been recorded only from the west of Africa (Angola to Cameroun), the above-mentioned specimens appear to belong to the same species. They are indistinguishable from the type, as are other specimens from Sibundeni, Zululand, preserved in the British Museum.

7. RANA OXYRYNCHUS Smith.

3 Amatongas; 1 Caia; 4 Charre; 2 Fambani River.

8. RANA MASCARENIENSIS Dum. & Bibr.

1 Caia; 1 Charre.

ABRANA, gen. n.

Pupil horizontal. Tongue free and deeply notched behind. Tympanum distinct. Fingers free; toes webbed, the outer metatarsals separated by web in their distal half; digits not dilated distally.

Maxillary teeth present; vomerine teeth in two short series close to the inner, anterior edge of the choanæ. Clavicles and procoracoids absent, replaced by a ligament; omosternum large, bony λ-shaped; sternum with a bony style. Terminal phalanges long and simple; no intercalary phalanges.

This genus is closely allied to *Ptychadæna*, with which it agrees in all respects except the condition of the shoulder-girdle. In *Ptychadæna* the clavicle and procoracoid are much reduced in comparison with the ancestral stock (*Rana*), and *Abrana* represents a stage further along the same line of degeneration. Whether *Ptychadæna* be regarded as a distinct genus or merely as a subgenus of *Rana*, the entire absence of the clavicle and procoracoid provides such a clear-cut differential character that the new form certainly seems worthy of the generic recognition. A parallel instance of the complete reduction of these two elements of the shoulder-girdle is furnished among the African Ranids by the genus *Cacosternum*.

9. ABRANA COTTI, sp. n.

Holotype a ♀, no. 1929.12.20.1 in the British Museum, from Charre.

Snout long, prominent, pointed, 1⅔ the diameter of the eye; canthus rostralis rounded; loreal region oblique, concave; nostril a little nearer the tip of the snout than the eye; interorbital space narrower than the upper eyelid. Tympanum distinct, ⅔ the diameter of the eye. Fingers pointed, with slight, fleshy, lateral fringes at bases of the three inner; first and second subequal; fourth a little longer than the second. Toes almost entirely webbed, the membrane reaching the terminal phalanges of all except the fourth, which has two phalanges free; a small inner but no outer metatarsal tubercle; a distinct diagonal tarsal fold. Tibio-tarsal articulation reaching the anterior border of the eye; heels strongly overlapping; tibia a little more than three times as long as broad, its length contained twice in the distance from snout to vent. Four moderately distinct glandular folds on each flank, the upper commencing from the posterior corner of the eye; mid-dorsal region with short, indistinct, longitudinal folds; a strong fold from beneath the eye to the shoulder; posterior portion of belly and hinder side of thighs slightly granular.

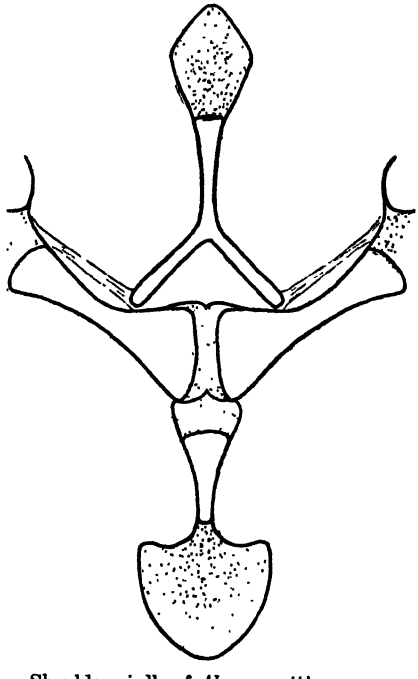
Brownish above, with small, darker spots; a dark line from nostril to eye; glandular fold in front of shoulder lighter. Thighs narrowly, tibia broadly, cross-banded; hinder side of thighs speckled with darker. Lower surfaces immaculate white.

Length from snout to vent 43 mm.; hind limb 65 mm.

Paratypes, 7 specimens from the type-locality.

These show some differences from the holotype. The tympanum may be slightly less than $\frac{2}{3}$ the diameter of the eye, the fleshy fringes at the bases of the fingers may be entirely absent, the tibio-tarsal articulation usually reaches to

Text-figure 1.



Shoulder-girdle of *Abrana cotti*, sp. n.

midway between the eye and the end of the snout, and the dorsal and lateral glandular folds are very inconstant, being often almost entirely absent.

Largest 40 mm. from snout to vent; smallest 30 mm.

All, including the holotype, show a lighter-coloured pineal spot on a level with the anterior borders of the eyes.

10. ARTHROLEPTIS STENODACTYLUS Pfeffer.

2 Amatongas.

11. PHRYNOBATRACHUS ACRIDOIDES (Cope).

11 Amatongas; 2 Charre; 14 Fambani River.

12. PHRYNOBATRACHUS NATALENSIS (Smith).

8 Amatongas.

POLYPEDATIDÆ.

13. CHIROMANTIS XERAMPELINA Peters.

4 Charre.

14. HYLAMBATES MACULATUS Dum.

1 Amatongas; 2 Caia.

15. LEPTOPELIS JOHNSTONI (Boulenger).

2 Charre; 8 Fambani River.

16. KASSINA SENEGALENSIS (Dum. & Bibr.).

3 Fambani River.

17. MEGALIXALUS BRACHYCNEMIS Boulenger.

3 Caia; 11 Fambani River.

Some of this series show differences from the typical colour-pattern; the dark dorsal stripe may be entirely wanting, the whole of the back then being silvery. What appears to be a valid differential character for the species is furnished by the distal subarticular tubercles of the two outer fingers, which are always double; a similar condition is often, but not constantly, found in the distal tubercle of the fourth toe.

18. MEGALIXALUS FORNASINII (Bianconi).

3 Caia; 3 Charre; 105 Fambani River.

Comparison of this large series with other specimens from different localities has revealed a considerable amount of confusion with regard to the synonymy and distribution of this species. Unfortunately, the most recent commentators on the species (Noble* and Barbour and Loveridge†) have made the same erroneous assumption, viz., that the form found in the Camerun-Gaboon-Congo region is the true *Megalixalus fornasinii*.

On the basis of this assumption Noble has denied Hewitt's statement‡ that *M. spinifrons* Cope (type-locality Umvoti, Natal) is synonymous with *M. fornasinii*, and has maintained the name for the form occurring in S.E. Africa. Barbour and Loveridge, finding a *Megalixalus* in Tanganyika Territory distinct from the West African form, referred it to *M. loveridgii* Procter, and suggested that possibly all records of *M. fornasinii* from the same region should be referred to *M. loveridgii*.

There is no doubt that there are two distinct species—the one occurring in the Rain Forest Region and the other in the Savannah Provinces of S. and E. Africa. The 166 specimens in the British Museum are readily separable into two groups corresponding to these two regions, and, since the type-locality of *fornasinii* is Mozambique, the East African species must receive that name and *M. dorsalis* (Peters)—type-localities Boutry, Dahomey, and Victoria, Camerun—must be reinstated for the Rain Forest species. The two forms are distinguishable thus:—

A. Skin of the back with small spines in both sexes; snout much longer than the eye; distance from nostril to eye at least ¾ the diameter of the latter; dark lateral streaks never in contact with the mid-dorsal stripe *M. fornasinii.*

B. Skin usually smooth, spines on the back only being found in breeding males; snout not longer than the eye; distance from nostril to eye less than ¾ the diameter of the latter; dark lateral bands usually in contact with the mid-dorsal stripe on the sacral region *M. dorsalis.*

The differences in the degree of spinosity and colour are exactly those which Noble has used to distinguish his so-called *fornasinii* (= *dorsalis*) from *M. spinifrons* Cope, and since the latter not only agrees in morphological characters with *fornasinii*, but also occurs within the range of that species, it is probable that Hewitt is correct in placing it in the synonymy.

* Bull. Am. Mus. Nat. Hist. xlix. (2) 1924, p. 274.
† Mem. Mus. Comp. Zool. Harvard, l. (2) 1928, p. 227.
‡ Ann. Natal Mus. ii. (4) 1913, p. 478.

The status of *M. loveridgii* also appears doubtful, but it is probable that it will be found to be not more than a local race of *fornasinii*. Barbour and Loveridge, in the very large series which they have reported upon (*loc. cit.*), find great variation in colour-pattern, their series showing all gradations from a uniformly coloured upper surface to the development of a well-defined dorsal, with indistinct lateral stripes. The majority of the present large series from Fambani River have three well-marked stripes as in typical *fornasinii*, but some have the lateral ones much less distinct than the dorsal, and in a few they are entirely absent; where this occurs the dorsal is only faintly indicated. Other specimens, again, in the British Museum, from Ngatana, Kenya, and Dodoma, Tanganyika Territory, have quite distinct lateral but no mid-dorsal stripes. Thus it appears that, as regards colour-pattern, *loveridgii* grades insensibly into *fornasinii*; the only other character which might distinguish *loveridgii* is the degree of webbing of the fingers. In the series of *fornasinii* examined, as in Barbour and Loveridge's collection, there is some variation in this respect, but no specimens appear to have quite as much as the type of *loveridgii*. The fingers of this latter specimen have, however, been drawn apart to their utmost extent, and retained there during fixation, and it is highly probable that this treatment has actually stretched the webbing and so produced a much exaggerated condition.

The synonymies and distributions of the two species, disregarding any local races which may be found to exist, will accordingly be:—

A. MEGALIXALUS FORNASINII (Bianconi).

Eucnemis fornasinii Bianconi, Spec. Zool. Mozambique, Rept. fasc. 2, p. 23, pl. v. fig. 1 (1850).

Rappia fornasinii Günther, Proc. Zool. Soc. London, 1868, p. 479.

Megalixalus fornasinii Boulenger, Cat. Batr. Sal. B.M. ii. p. 130 (1882) (part); Peters, Reise Nach Mossambique, iii. 1882, p. 160, pl. xxiv. fig. 2, pl. xxvi. fig. 6; Pfeffer, Jahrb. Hamburg Wiss. Anst. vi. 2, 1889, p. 10; Boulenger, Ann. Mag. Nat. Hist. (6) vi. 1890, p. 93; Müller, Verh. Natf. Ges. Basel, viii. 1890, p. 257; Boulenger, Proc. Zool. Soc. London, 1891, p. 308; Boettger, Kat. Batr. Mus. Senck. p. 21 (1892); Pfeffer, *op. cit.* x. 1893, p. 99; Gunther, *op. cit.* 1894, p. 88; Bocage, Jorn. Sci. Lisbon (2), iv. 1896, p. 101; Tornier, Kriechthiere Deutsch-Ost-Afr. p. 156 (1896); Gunther, *op. cit.* 1897, p. 801; Johnston, British Central Africa, ed. i. p. 361 *a* (1897); Tornier, Arch. Naturg. lxiii. i. 1897, p. 66; Mocquard, Bull. Mus. Nat. Hist. Paris, v. 1899, p. 219; Boulenger, Proc. Zool. Soc. London, 1900 (2), p. 445 (part); Nickel, Helios, xviii. 1901, p. 72; Mocquard in Foà, Res. Sci. Voy. Afr. Foà, p. 558 (1908); Boulenger, Ann. S. Afr. Mus. v. 1910, p. 531 (part); Lönnberg in Sjöstedt, Kilimandjara-Meru Exp. i. (4) p. 25 (1910); Hewitt, Rec. Alb. Mus. ii. 1911, p. 224; Boettger in Voeltzkow, Reise in Ost-Afr. iii. p. 346 (1913); Hewitt, Ann. Nat. Mus. ii. 1913, p. 479; Nieden, Mitt. Zool. Mus. Berlin, vii. 1915, p. 372 (part); Noble, Bull. Am. Mus. Nat. Hist. xlix. 1924, p. 274 (part).

Hyperolius bivittatus Peters, Arch. f. Naturg. 1855, p. 56.

Megalixalus spinifrons Cope, Proc. Ac. Philad. 1862, p. 342; Boulenger, Cat. Batr. Sal. B.M. (2) p. 130 (1882); Hewitt, Rec. Albany Mus. ii. (4) 1912, p. 280.

Megalixalus fornasinii var. *unicolor* Boettger in Voeltzkow, Reise in Ost-Afrika, iii. p. 349 (1913).

Megalixalus loveridgii Procter, Proc. Zool. Soc. London, 1920, p. 418; Rept. Add. Men. Zool. Soc. London, 1927, p. 9; Barbour & Loveridge, Mem. Mus. Comp. Zool. Harvard, l. (2) 1928, p. 227.

Type-locality.—Mozambique.

Distribution.—Kenya, Pemba, Zanzibar, Tanganyika Territory, Portuguese E. Africa, Nyasaland, Natal, and Cape Province, S. Africa.

Specimens examined.—Ngatana (1), Zanzibar (2), Dodoma (1), Morogoro (1), Mozambique (2), Caia, Port. E. Africa (3), Charre, Port. E. Africa (3), Fambani River (105), Delagoa Bay (1), "Zambesi" (4), Nyika Plateau, Shire Valley, Chiromo, and "Kondowe to Karonga," Nyasaland (21).

B. MEGALIXALUS DORSALIS (Peters).

Hyperolius dorsalis (Schleg.) Peters, Mon. Berlin Ak. 1875, p. 206, pl. i. fig. 2.

Megalixalus fornasinii (non Bianconi) Boulenger, Cat. Batr. Sal. B.M. (2) p. 130 (1882) (part); Werner, Verh. zool.-bot. Ges. Wien, xlviii. 1898, p. 195; Boulenger, Proc. Zool. Soc. London, 1900, ii. p. 445 (part); Andersson, Ark. Zool. Stockholm, ii. (20) 1905, p. 18; Boulenger, Ann. Mus. Genova, (3) ii. 1905 (1906), p. 166; Andersson, Jahrb. Nassau. Ver. Naturk. lx. 1907, p. 238, figs. 1–3; Nieden, Mitt. Zool. Mus. Berlin, iii. 1908, p. 504; Boulenger, Ann. S. Afr. Mus. v. 1910, p. 531 (part); Müller, Abh. Bayer. Ak. Wiss. 2 Kl. xxiv, 1910, p. 625; Nieden, Fauna Deutsch Kolon. (1) 2, 1910, p. 58, figs. 121–123; Barbour, Bull. Mus. Comp. Zool. Harvard, liv. (2) 1911, p. 134; Lampe, Jahrb. Nassau. Ver. Naturk. lxiv. 1911, p. 215; Chabanaud, Bull. Mus. Nat. Hist. Paris, 1919, p. 457; Bull. Com. Et. Hist. Sci. A.O.F. 1921, p. 459; Noble, Bull. Am. Mus. Nat. Hist. xlix. 1924, p. 274 (part), pl. xli. fig. 1.

Megalixalus schnciderі Boettger, Ber. Senck. Ges. 1889, p. 276.

Type-localities.—Boutry, Dahomey, and Victoria, Camerun.

Distribution.—French Guinea, Liberia, Gold Coast, Ashanti, Dahomey, Fernando Po, Camerun, Gaboon, French Congo, Belgian Congo, Uganda.

Specimens examined:—Gold Coast (1), Ashanti (3), Fernando Po (2), Camerun (10), Gaboon (1), French Congo (7), Uganda (1).

19. HYPEROLIUS CONCOLOR (Hallowell).

1 Caia; 4 Charre.

20. HYPEROLIUS MARMORATUS Rapp.

3 Charre; 10 Fambani River.

21. HYPEROLIUS BAYONI (Boulenger).

1 Charre; 102 Fambani River.

This large series agrees perfectly in morphological characters and general habits with typical specimens of the species. The colour-pattern, too, is similar, but many specimens, in addition to the lateral and mid-dorsal dark stripes, have a dorso-lateral streak, more distinct posteriorly than anteriorly, which is not indicated in the type series; when this is present, the median stripe, faint in typical specimens, is very strongly marked. Although the species has not hitherto been recorded south of Kenya, at least under this name, the Zambesi and Kenya frogs are probably conspecific.

22. HYPEROLIUS ARGUS Peters. (Pl. I. figs. 2–8.)

8 Caia; 86 Fambani.

This large series shows great uniformity in all morphological characters, but is subdivisible into two extraordinarily different colour varieties. These two groups are as follows:—

(i.) 27 specimens, with the typical *argus* colour-pattern of a pink, black-bordered canthal streak which extends on to and includes the upper eyelid and a greater or less number of large similarly-coloured ocelli irregularly scattered on the back and flanks; ground-colour whitish to pale brown. (In life the colour is pale brown to chocolate or purple with bright orange or yellowish, black-bordered ocelli and canthal streaks.) (Pl. I. figs. 7 & 8.)

The largest specimen measures 32 mm. and the smallest 20 mm.; all are *adult females* with well-developed ovaries.

(ii.) 62 specimens, pale straw-coloured or whitish above, with a dusky canthal streak, sometimes a little black stippling or a few small black dots on the back and a more or less distinct narrow silvery line from the posterior corner of the eye to the groin; occasionally this stripe borders the edge of the eyelid and extends forwards along the canthus rostralis. (In life the upper surfaces are pale green and the lateral line golden.) (Pl. I. figs. 2 & 3.)

Of this series 30 are more or less *adult males* with vocal sacs; the larger have these sacs fully developed, with a large external "adhesive disc" beneath the throat, and the smaller, though without any external evidence of the sacs, have the openings visible on the floor of the mouth. Largest 28 mm., smallest 20 mm.

The remaining 32 prove, on dissection, to be immature, with the sexes equally represented; 16 are males, with the invagination of the vocal sacs scarcely, or not, begun, and a similar number are females, with very immature ovaries and very small oviducts. The largest measures 22 mm. and the smallest 14.

In addition there are five specimens, from 19 to 23 mm. long, which show transitional stages between the two colourings. Proceeding from the second type described above, the first stage is the reduction of the silvery lateral line and the appearance of some irregular dusky patches on the back. At the same time the dark canthal streak broadens, and then a centrifugal movement of the black pigment occurs in both the dorsal spots and the canthal streak. At first the ocelli thus produced are bordered only by an indefinite dotted line, and the central area is of the same general colour as the rest of the dorsum. Finally, however, the pink or orange pigment appears, the dark margins become more definite, and the typical coloration of the first type is produced. (Pl. I. figs. 4–6.)

There is only one possible explanation of these facts, viz., *Hyperolius argus* exhibits a marked sexual dichromatism, the males retaining the juvenile colour-pattern and females assuming a distinctive livery at the onset of sexual maturity, which is reached at a length of about 19–23 mm. The series of specimens examined is too large to admit of any possibility of coincidence, and, moreover, the relative numbers of the sexes are normal. In brief, the analysis of the collection is:—

Males.	*Females.*
30 adults; colouring (ii.). Lengths, 20–28 mm.	27 adults; colouring (i.). Lengths, 20–32 mm.
	5 adolescents; colour intermediate between (i.) and (ii.). Lengths, 19–23 mm.
16 juveniles; colouring (ii.). Lengths, 14–22 mm.	16 juveniles; colouring (ii.). Lengths, 14–22 mm.

This discovery raises some complications with regard to the synonymy of the species. In the first place it is almost certain that the males and juveniles have been hitherto regarded as a species distinct from the females. In the present unsatisfactory condition of the genus, however, it is almost impossible to be sure of the correct status of any species without seeing typical or topotypical material. Nevertheless it seems possible that *Hyperolius pusillus* (Cope), originally described from Natal (which is within the range of *H. argus*), was based on a male of *H. argus*. The very brief description agrees quite well with a male of this species, particularly as regards size, colour, and the condition of the vocal sacs; no mention is made of the silvery dorso-lateral line, but this is often quite inconspicuous.

More recently Barbour and Loveridge* have described a large series of frogs from the Uluguru Mountains as *Hyperolius argus*, but this series exhibits no sexual

* *Tom. cit.* p. 222.

dichromatism, and the colour-pattern of the adult is derived in quite a different way from that described above. Thanks to Dr. Barbour's courtesy, I have been able to examine a series of these Uluguru frogs (10) and also a series of *Hyperolius puncticulatus* (Pfeffer) from Amani and Phillipshof. There is no doubt that the Uluguru "*argus*" is not conspecific with the frog here recorded under the same name, and the present determination appears to be the correct one. The series from Tanganyika Territory, as Barbour and Loveridge have pointed out, differs from the description of the species in the possession of a slightly longer snout and in having the light, black-edged marking in the form of a streak, from the nostril, above the eye, toward the groin, and confined to the anterior half of the body; any ocellar spots are in the position of a continuation of this streak, and are never scattered over the dorsum. The present series, however, has constantly a shorter snout (orbital diameter longer than distance from eye to nostril, and usually about as long as the snout), there are always ocelli on the dorsum (as figured by Peters), and the toes are more fully webbed. Comparison shows that the morphological features of the Uluguru series are those of *H. puncticulatus* Pfeffer, and in view of the "intermediates" recorded from Phillipshof * it seems probable that they ought to be regarded as a colour variety or a local race of that species.

23. HYPEROLIUS MOSSAMBICUS, sp. n. (Pl. I. fig. 1.)

Holotype a ♂, no. 1929.12.20.312 in the British Museum, from Fambani River, Mozambique.

Head as long as broad; snout vertically truncate, not prominent, a little longer than the diameter of the eye; canthus rostralis rounded; loreal region nearly vertical; nostril much nearer the tip of the snout than the eye; interorbital space twice as broad as the upper eyelid; tympanum hidden. Digital dilatations small, the largest not more than once and a half as broad as the penultimate phalanx. Fingers with merely a rudiment of web, the first shorter than the second, which is shorter than the fourth. Toes about ½-webbed, two phalanges of the three inner, three of the fourth, and one of the fifth free; fifth a little longer than the third. Subarticular tubercles well developed; a small inner, but no outer, metatarsal tubercle. Tibio-tarsal articulation reaching slightly beyond the anterior corner of the eye. Skin smooth above, granular beneath, more pronouncedly so posteriorly.

Pale brown above, with darker markings and dots. A narrow dark streak from the nostril to the eye, continued rather indistinctly behind from the posterior corner of the eye towards the groin; a large dorsal marking commencing between the eyes, where it connects the upper eyelids, narrowing on the nape, broadening abruptly to its original width, and then bifurcating; the branches taper regularly and extend onto the sacral prominences. Remainder of the back and limbs irregularly stippled with darker. Lower surfaces uniformly white.

A large subgular vocal sac, with a median subgular disc.

Length from snout to vent 24 mm. Hind limb 38 mm.

The three paratypes, nos. 1929.12.20.309–311 in the British Museum, from the type-locality, are essentially similar to the preceding. The general coloration has a greenish tinge, and in one the fifth toe is equal to the third.

This species differs from the majority of the species of *Hyperolius* in the reduced amount of webbing between the fingers and toes. This character distinguishes it from *H. cinctiventris* Cope and *H. symmetricus* (Mocquard), which have a similar colour-pattern, but its nearest relative appears to be *H. granulatus* (Boulenger), with which it agrees not only in the amount of digital webbing, but also in its short truncate snout and the position of the nostrils close to the tip of the latter. It is readily distinguished, however, by the completely smooth skin of the upper surfaces and the totally different colour-pattern.

* Barbour and Loveridge, *tom. cit.* p. 220.

24. HYPEROLIUS MICROPS Gunther.

4 Fambani River.

BUFONIDÆ.

25. BUFO REGULARIS REGULARIS Reus.

2 Amatongas; 2 Caia; 2 Charre; 2 Fambani River.

PIPIDÆ.

26. XENOPUS LÆVIS (Daudin).

4 Amatongas.

27. XENOPUS MÜLLERI (Peters).

3 Amatongas; 3 Fambani River.

In addition to the length of the tentacle and the prominence of the metatarsal tubercle, which are usually used to distinguish the latter two species, it may be noted that the vomerine teeth and the coloration also seem to provide good differential characters, thus:—

(i.) Vomerine teeth absent; dark grey above, sometimes mottled but not spotted; white beneath, the thighs only slightly stippled with brown *X. lævis.*

(ii.) Vomerine teeth present; more or less distinct, insuliform, dark spots arranged in irregular longitudinal series above; lower surfaces more or less heavily stippled and spotted with blackish *X. mülleri.*

BREVICIPITIDÆ.

28. HEMISUS MARMORATUM (Peters).

2 Charre; 6 Fambani River.

29. BREVICEPS MOSSAMBICUS Peters.

2 Charre.

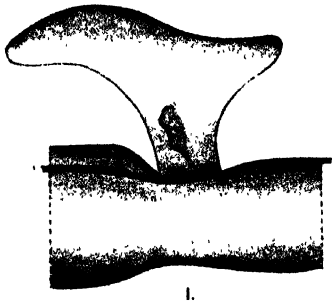
EXPLANATION OF THE PLATE.

Fig. 1. *Hyperolius mossambicus*, sp. n.

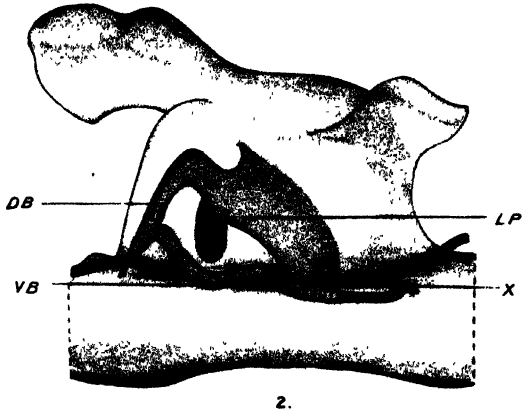
Figs. 2 & 3. *Hyperolius argus* Peters, adult males.

4, 5, & 6. *Hyperolius argus* Peters, immature females showing stages in the development of the adult coloration.

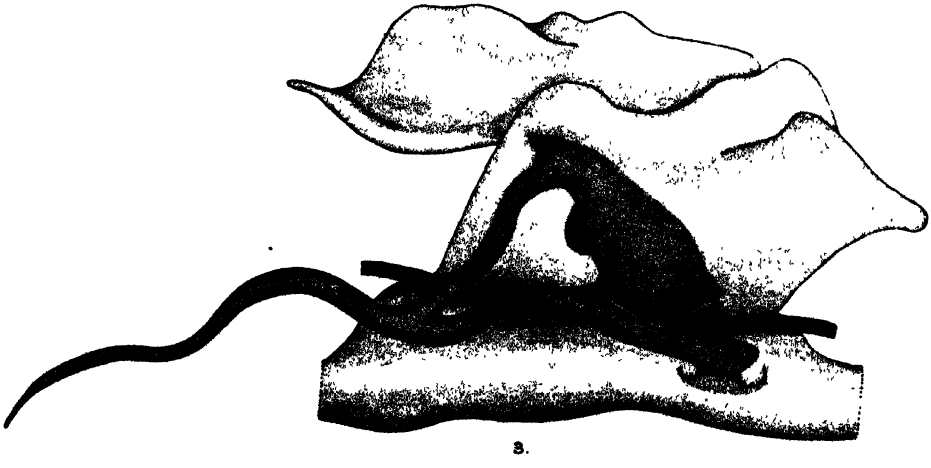
7 & 8. *Hyperolius argus* Peters, adult females.



1.



2.



3.

John Bale, Sons & Danielsson, Ltd., London.

RECONSTRUCTIONS OF VERTEBRÆ OF *TRITON VULGARIS*.

42. The Attachments of the Urodele Rib to the Vertebra, and their Homologies with the Capitulum and Tuberculum of the Amniote Rib.

By PETER GRAY, B.Sc., A.R.C.S.*

(From the Zoological Research Laboratory, Imperial College of Science.)

[Received May 20, 1930: Read October 21, 1930.]

(Plate I.† ; Text-figures 1 & 2.)

The exact points of insertion of the urodele rib appears to have given rise to a good deal of confusion. Though the result of this confusion pertains only to the rib, the cause involves also the lateral process, a bifid structure to whose terminal ends the dorsal and ventral roots of the rib are usually supposed to be "articulated." This word is advisedly placed between quotation marks for reasons which will become apparent in the course of this paper.

It is not the intention of the present writer to enter into a lengthy discussion of the historical side of the question, for such a discussion is to be found in the work of Mayerhofer; a brief analysis of the situation as left by this worker, however, would not be out of place. Both Mayerhofer and Göppert regarded the primitive type of urodele lateral process as having two connections with the vertebra. The dorsal connection was naturally to the lateral portion of the neural arch, but the ventral was to the side of the chorda; such a condition is well shown by Göppert's figure of the young *Necturus* larva. This, however, was only the most primitive type; passing on to *Salamandra*, we find that the lateral process is now regarded as having both a dorsal and ventral attachment to the neural arch, while the previous connection to the chorda remains, in "die neugeborene larve" as "ein letzter knorpeliger Rest." We are here given, then, the primitive and advanced stages of an evolutionary series whose intermediate stages are unfortunately ignored; "unfortunately," since they are singularly difficult to comprehend. Leaving aside any question of probability, we may, on the existing data, postulate two lines of evolution:—

i. That the ventral attachment of the lateral process became reinforced by a dorsally directed attachment to the neural arch, giving a condition in which the lateral process had three points of attachment; of these three the primitive attachment to the chorda degenerated.

ii. That the ventral attachment to the chorda gradually passed round and up on to the neural arch.

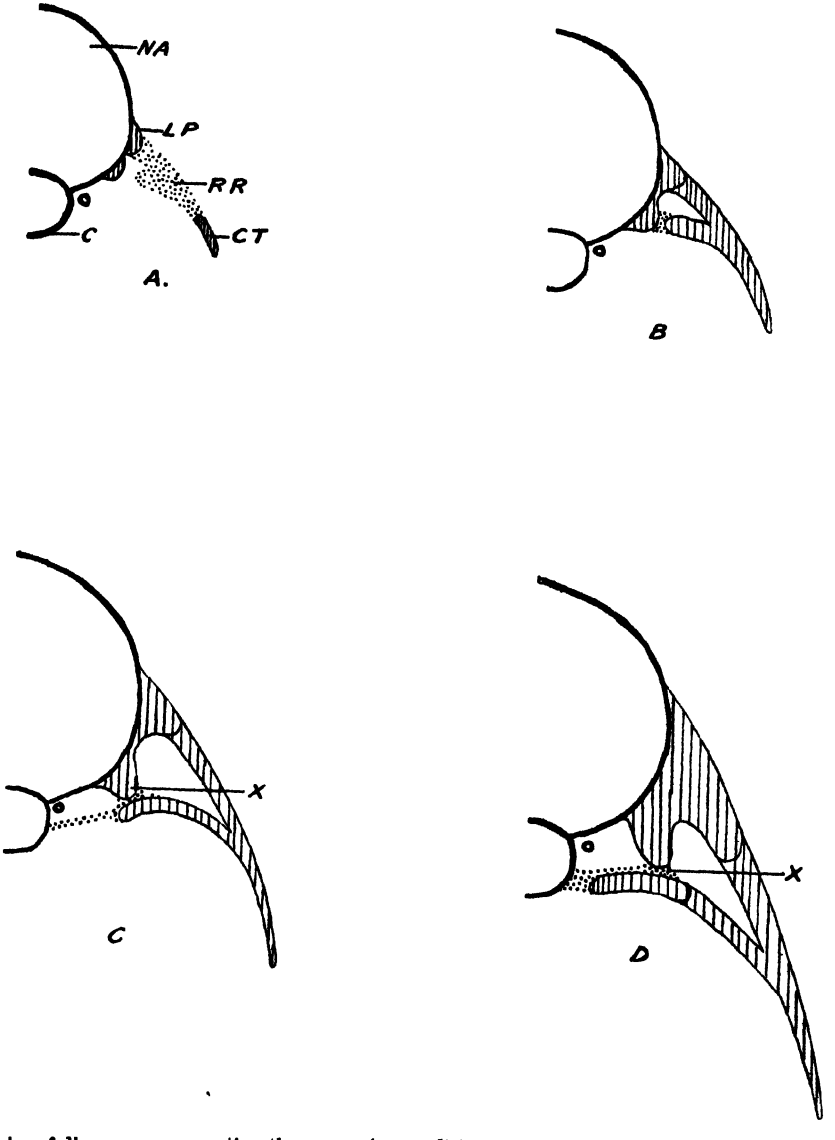
This later suggestion appears fairly simple, provided that we totally ignore the existence of both the vertebral artery and the vertebral vein. Both these, in *Necturus*, lie enclosed between the dorsal and ventral attachments of the lateral process, while in *Salamandra* they lie ventrally to both attachments. If, therefore, we are to believe that the ventral attachment to the chorda passed up on to the neural arch, we must also believe that in so doing it passed *through* the vertebral blood-vessels—a morphological impossibility.

Before proceeding to a consideration of the first (singularly improbable) line of evolution suggested above, it would be as well to consider the condition in a previously almost ignored urodele—*Triton vulgaris*.

* Communicated by Prof. E. W. MACBRIDE, F.R.S., F.Z.S.

† For explanation of the Plate, see p. 911.

Text-figure 1.



Series of diagrams representing the successive conditions of the ribs and lateral process in *Triton vulgaris*. A, C, and D correspond respectively to the conditions shown in Pl. I. figs. 1, 2 and 3.

C. Chorda. C.T. Chondrified tip of rib rudiment. L.P. Lateral process. N.A. Neural arch. R.R. Rib rudiment. X. Connective-tissue connection between ventral root of rib and lateral process.

Stage 1.

This stage, of which one vertebra is shown in the reconstruction on Pl. I. fig. 1, is about half-way between hatching and metamorphosis. The lateral process is represented by two small agglomerations of cartilage cells lying against the side of the neural arch. The "rib" is at this stage still a collection of mesenchyme cells lying in the sheet of connective tissue between the two myotomes. In support of Mayerhofer's contention that chondrification emanates from the distal end of the rib inwards, we find that a small number of cells from the extreme tip of the elongate agglomeration are becoming swollen and hyaline.

A diagrammatic representation of the condition at this stage is shown at A (text-fig. 1). It should be especially noticed that the ventral rudiment of the developing lateral process has, as yet, no connection with the connective-tissue rudiment of the ventral head of the rib.

Stage 2.

This stage, one vertebra from which is represented on Pl. I. fig. 2, is approximately a fortnight before metamorphosis. The lateral process is now well developed, and consists of a cartilaginous mass inserted upon the lateral surface of the neural arch. The latero-dorsal point of this cartilaginous mass is continued backwards and outwards as the dorsal branch (D.B.) of the developing rib; there is no sign whatever of any form of "articulation" between the rib and the lateral process, which are apparently one sold cartilaginous mass. The latero-ventral point of the lateral process is not, however, fused to the ventral branch (V.B.) of the developing rib; the two pieces of (blue) cartilage are connected (at X) by (yellow) connective tissue, but there is no fusion whatever of the cartilaginous elements. The most anterior (proximal) end of the rib is definitely anterior to the lateral process, and is prolonged as a sheet of connective tissue (yellow), which is inserted upon the dorso-lateral surface of the chorda. The vertebral artery (red) runs between the ventralmost point of insertion of the lateral process and the attachment of the connective-tissue prolongation from the lower branch of the rib to the chorda.

This state of affairs is diagrammatically summed up in "C" (text-fig. 1). Now it seems to the writer quite impossible to regard the point X as the insertion of the rib, since this latter quite definitely projects beyond the lateral process. Neither can, at this stage, the chordal connective-tissue junction be regarded as a true insertion, since there is no definite socket yet developed. Let us now examine a post-metamorphic condition.

Stage 3.

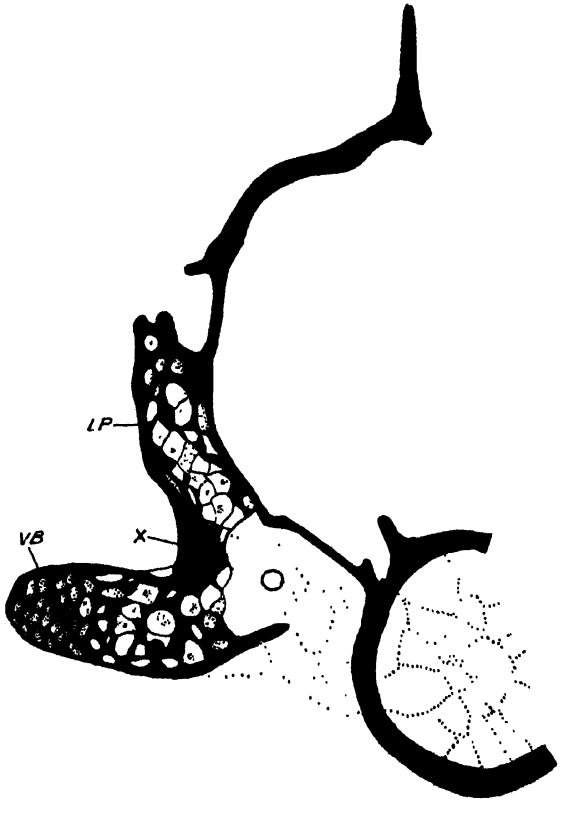
The vertebra represented in Pl. I. fig. 3 is from a newt about one month after metamorphosis. The lateral process is in very much the same condition that it was in the last stage investigated, save that it is now rapidly becoming ossified. The dorsal branch of the rib is beginning to show signs of an articulation at the point indicated in the figure. The ventral branch of the rib has increased in length still further beyond the ventralmost edge of the lateral process, to which it is still attached by a sheet of connective tissue (yellow), both the cartilaginous masses, as well as the connective-tissue junction, showing signs of ossification. A camera lucida drawing of a section of this region is represented in text-fig. 2, in which the connective-tissue junction X between the lateral process (L.P.) and the ventral rib branch (V.B.) is clearly apparent. Returning to the reconstruction, we see that the most anterior point of the ventral branch of the rib is firmly joined to the chorda by a link of connective tissue, rapidly becoming ossified. The beginnings of an articulation are becoming apparent upon the rib, just before the beginning of the connective tissue with the lateral process.

Text-fig. 1, D, shows this stage reduced to a theoretical diagram, with the aid of which we may proceed to a discussion of the exact points of attachment of the rib.

Discussion.

In this relation we must return for one moment to the hypothesis which we obtained in the introduction from previously published material. This hypothesis was to the effect that if we were to regard the connection of the ventral rib head

Text-figure 2.



Camera lucida drawing of one of the sections from which Pl. I. fig. 3 was reconstructed to show the independence of the cartilage masses forming the lateral process and ventral rib root.

L.P. Lateral process. V.B. Ventral root of rib. X. Connective-tissue (ossified) connection between the two.

to the chorda in the young Salamander as a remnant, we must regard the connection to the lateral process as an evolved structure of primary importance. In the light of *Triton* such a hypothesis becomes even more improbable than before; for here we find that in the young larva there is no trace of the chordal connection, but that this connection later develops and finally becomes ossified—

hardly the behaviour of a degenerating remnant. Surely it is more probable that the connection to the chorda is of fundamental importance, while the ventral connection to the lateral process is a secondarily derived structure? *Necturus*, seen in this light, still remains the primitive type; but we are left at a loss to explain the lateral process "articulation" of the ventral rib in *Salamandra*. Yet we may be permitted to question whether or not such an "articulation" actually exists. An examination of the adult vertebra of *Triton* would certainly leave one with the impression that the ventral articulation of the rib was with the lateral process. It is only when we examine a developmental stage that we find the clear line of demarcation existing between ventral rib and lateral process; it is only in this stage, in fact, that we realise the true insertion of the *articulated portion* of the rib to be on the chorda. Leaving aside any question of "articulations," we may say that the dorsal and ventral roots of the rib abut on the lateral process and chorda respectively; the articulations are formed later, and their position along the course of the urodele rib is no indication whatever of the homologies of the rib attachments.

If once we accept this interpretation of the attachments of the urodele rib, there remains no difficulties in the way of correlating such a rib with the amniote type. What has been referred to throughout as the ventral root of the rib becomes, under amniote terminology, the capitulum, while the dorsal rib root becomes the tuberculum. In fact, the acceptance of the interpretation given in this paper permits not only of the correlation of one urodele rib type with another, but also the correlation of a fundamental urodele type with the corresponding amniote structure.

In conclusion, I would wish to express my gratitude to Professor E.W. MacBride, F.R.S., not only for the great assistance which he has given me in the preparation of this paper, but also for the original suggestion that it should be commenced.

Bibliography.

Göppert, E. (1895). Zur Kentniss der Amphibienrippen. Morph. Jahrb. xxii.

Mayerhofer, F. (1909). Untersuchungen über die Morphologie und Entwickelungsgeschichte des Rippensystems der Urodelen Amphibien. Arb. Zool. Inst. Univ. Wien, xvii.

EXPLANATION OF THE PLATE.

Plate I.

Fig. 1. Graphic reconstruction from transverse sections of one vertebra from a larva of *Triton vulgaris*, aged about six weeks.

2. Graphic reconstruction from transverse sections of one vertebra of a larva of *Triton vulgaris*, aged about ten weeks.

3. Graphic reconstruction from transverse sections of one vertebra from a young specimen of *Triton vulgaris*, killed about one month after the completion of metamorphosis.

D.B. Dorsal root of rib. L.P. Lateral process. V.B. Ventral root of rib. X. Line of demarcation between ventral root of rib and lateral process.

(All three reconstructions have the uniform magnification of 70.)

Colour indications:—

Red Vertebral-artery.
Blue ... Cartilage.
Yellow... Connective tissue.

43. Report on the Hydracarina. Mr. Omer-Cooper's Investigation of the Abyssinian Fresh Waters (Dr. Hugh Scott's Expedition). By Dr. C. WALTER *.

(From the Zoological Department, University of Basel.)

[Received February 4, 1930: Read October 21, 1930.]

(Text-figures 1–18.)

INTRODUCTION.

The collection of Hydracarina described below was submitted to me for examination through the kindness of Mr. J. Omer-Cooper, who collected them during the Scott Omer-Cooper expedition to the Abyssinian Plateau. Amongst the chief objects of this expedition were the study of the fauna in relation to the conditions of isolation existing in the region, and an attempt to trace the origin of the various components of the fauna and to arrive at some idea as to the extent to which tropical forms, migrating into temperate regions, have become modified in the new habitat. This collection of Hydracarina, the first made in Abyssinia, can, unfortunately, add little to the solution of these problems. It comprises but seven species, of which five are new, and no doubt represents but a small proportion of the Hydracarina fauna of the country as a whole. Moreover, so far as this group of animals is concerned, the environs of the Abyssinian highlands must be regarded as practically unknown. The water-mite fauna of the high-lying regions of East Africa has been so little explored that only that of the Mount Elgon region (Lundblad, 1927) is sufficiently well known to be available for comparison. The Mount Elgon species are, however, chiefly torrenticoles, whilst, on the other hand, those from Abyssinia are all stagnant-water forms, so that no value attaches to such a comparison.

The Hydracarina in this collection were all obtained from four localities, as follows:—

1. Djem Djem Forest, pond no. 2; 26th Sept., 1926; altitude, 8100 ft. A small, semi-permanent pond having no outflow.

Piona angulata Viets, 8 ♀ ♀.
Arrhenurus procerus, sp. n., 2 ♀ ♀.
Arrhenurus iniquus, sp. n., 10 ♀ ♀.

2. Wouramboulchi, Serpent Lake and the surrounding marshes; 2nd–5th October, 1926; altitude, 9000 ft. This is the source of one of the affluents of the Blue Nile.

Hydrarachna eldoretica Lundblad, 1 nymph.
Limnesia rugosa, sp. n., 62 ♀ ♀, 1 nymph.
Piona crassipes, sp. n., 15 ♂ ♂, 21 ♀ ♀, 28 nymphs.
Arrhenurus iniquus, sp. n., 1 ♀.

* Translated and communicated by J. OMER-COOPER, M.A., F.L.S., C.M.Z.S.

3. Lakes of Addas, Hora Bishoftu, 2nd Dec., 1926; altitude, *circa* 7500 ft. A small crater-lake, slightly saline, and having no outflow.

Hydrarachna spinosa Koenike, var. *subtilis* var. n., 21 ♂♂, 20 ♀♀, 3 nymphs.

4. Lakes of Addas, Hora Harsadi; 2nd Dec., 1926; altitude, *circa* 7500 ft. A small crater-lake, slightly saline, and having no outflow.

Hydrarachna spinosa Koenike, var. *subtilis* var. n., 7 ♂♂, 5 ♀♀.

The distribution of the species in Abyssinia is shown in the following table:—

	Djem Djem Forest, Pond no. 2, 8100 ft.	Wouramboulchi, Serpent Lake and Marshes, 9000 ft.	Lakes of Addas, Hora Bishoftu, 7500 ft.	Lakes of Addas, Hora Harsadi, 7500 ft.	Total.
Hydrarachna eldoretica	—	1	—	—	1
„ *spinosa* var. *subtilis*	—	—	44	12	56
Limnesia rugosa	—	63	—	—	63
Piona crassipes	—	64	—	—	64
„ *angulata*	8	—	—	—	8
Arrhenurus procerus	2	—	—	—	2
„ *iniquus*	10	1	—	—	11
Individuals. Total...	20	129	44	12	205

Such slight information naturally admits of neither biological nor faunistic conclusions. It only shows that *Limnesia rugosa* and *Piona crassipes* are probably the commonest species in the Serpent Lake, and that in Hora Bishoftu and Hora Harsadi, where the salinity of the waters is considerable, only one species seems capable of existing. *Hydrarachna spinosa* var. *subtilis* was the only form obtained, and was taken from both these lakes in relatively large numbers, and must, therefore, be a species adapted to the conditions of alkaline salinity found there.

For the moment the geographical diffusion of the following species is limited to the Abyssinian Plateau:—

Limnesia rugosa, sp. n.
Piona crassipes, sp. n.
Arrhenurus procerus, sp. n.
Arrhenurus iniquus, sp. n.

The three remaining species are found in other parts of Africa as follows:—

Hydrarachna eldoretica Lundblad: was found in a small lake at an altitude of 2–3000 m. on the plateau north of Eldoret in the Mt. Elgon region (*Lundblad*, 1927).

Hydrarachna spinosa Koenike: the typical form was described by Koenike (1893) from a marsh at Mathews, in Zanzibar. The *subtilis* variety I have recently found in collections from the Sahara.

Piona angulata Viets, 1921: is the most widely distributed species, having a wide horizontal spread and also a considerable vertical distribution. Viets, 1921, reports it from a small freshwater lake at the Elanairobi crater in the West Masai Steppe; and in a mud sample from Galago Lake, north-west of Ruanda.

Lundblad, 1927, records it in large numbers from the same locality as *Hydrarachna eldoretica*, and also in a small crater-lake on the summit of Mt. Elgon at an altitude of 4200 m. This species may therefore be considered a typical eurythermic form.

Description of the Species.

Hydrarachna spinosa Koenike, var. subtilis var. n.

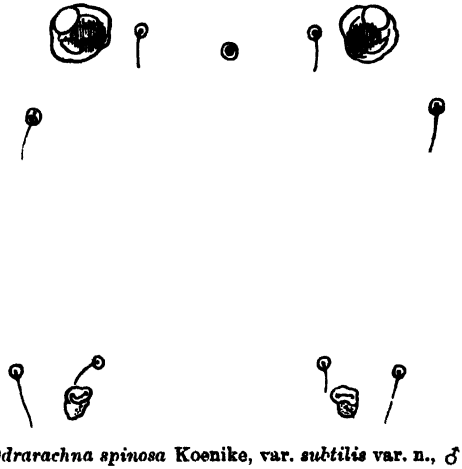
Localities.—Addas, Hora Bishoftu, *circa* 7500 ft., 2nd Dec., 21 ♂, 20 ♀, 3 nymphs; Addas, Hora Harsadi, *circa* 7500 ft., 2nd Dec., 7 ♂, 5 ♀.

Remarks.—This new variety is so close to the type of *H. spinosa* Koen. that at first it was believed that the Abyssinian and East African forms were identical. Koenike, 1893, p. 43, based his description upon a single male specimen, and although his account is somewhat defective, omitting several important diagnostic characters, the Abyssinian material is enough to show that definite and stable variations exist sufficient to justify their separation from the type as a named variety.

Description.

Male.—Size of body reaches 2·7 mm. (*i.e.* a little larger than the type); contours rounded; colour red. The skin is densely covered with short thorn-like papillæ, some of which have have a short, sharp, backwardly-directed apex. The anterior dorsum has a small, round, chitinous plate, for the attachment of muscles, at a distance of 660 μ from each double eye; anterior to the edge of this plate are two setæ (text-fig. 1). Koenike does not mention these structures in his description

Text-figure 1.



Hydrarachna spinosa Koenike, var. *subtilis* var. n., ♂.
Dorsal surface showing eyes and setæ, etc.

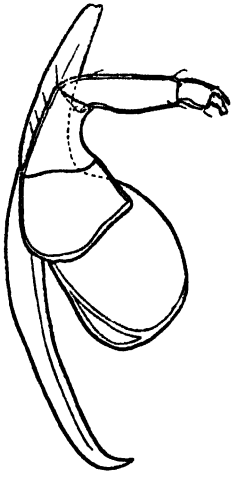
of the type-form. The double eyes lie at a distance of about 400 μ apart and are smaller than in the East African form, having a diameter of only 150 μ. There is a seta behind each eye capsule and one near to its median edge. The median eye is in the centre of a chitinous ring surrounded by soft skin.

Capitulum: 965 μ in length, with the rostrum curved downwards.

Mandible: 945 μ in length, shorter than in the type; the sharp-pointed anterior region bears a row of short blunt teeth flattened at the top.

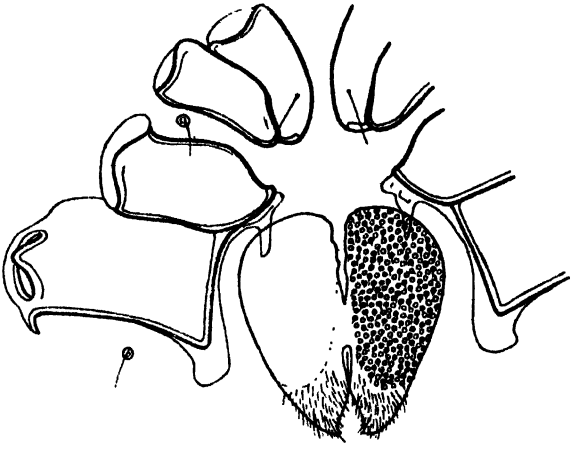
Palp (text-fig. 2): in every case the palps are longer than in the type, where they do not project beyond the extremity of the rostrum, whereas in this form

Text-figure 2.



Hydrarachna spinosa Koenike, var. *subtilis* var. n., ♂. Palp.

Text-figure 3.



Hydrarachna spinosa Koenike, var. *subtilis* var. n., ♂. Epimera and genital area.

both the end-organs and part of the third segment project. The appearance and armature of the segments, which are not described by Koenike for the type, are seen in text-fig. 2.

The measurements of the segments are as follows:—

Segment ...	1	2	3	4	5
Length.....	195 μ	210 μ	260 μ	120 μ	45 μ
Height	250 μ (max.)	165 μ (prox.)	95 μ (dist.)	85 μ (max.)	60 μ

Epimera (text-fig. 3): 900 μ long and 1860 μ broad; strongly resembling those of the type-form except that the 4th plate has a subcutaneous prolongation of the posterior median angle.

Legs: anterior, 1185 μ in length; posterior, 2205 μ in length. The anterior legs are not particularly short, as they are in the form described by Koenike.

Genital area (text-fig. 3): is considerably longer than it is broad (length 600 μ, breadth 525 μ) and somewhat smaller than in the type. The plates are narrowly separated anteriorly for a distance of 250 μ—the East African form has an angular notch only. As in the type, both the plates are covered with acetabula, of which about half have a short fine hair inserted in the centre of the pore. There are somewhat longer hairs, very dense on the sides of the genital sulcus, which are not surrounded by acetabula. The genital sulcus has a length of about 180 μ.

Anus: nearer to the genital plate than in the type-form, the distance being only 150 μ, whereas in the type it is 200 μ. It is surrounded by a ring of chitin.

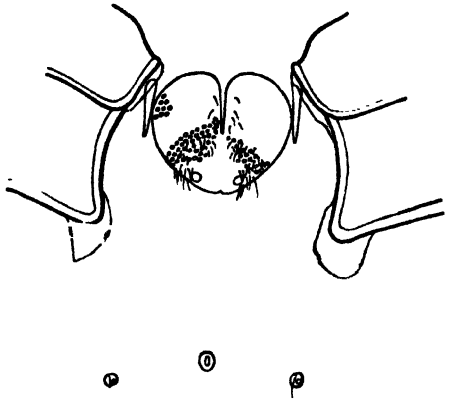
Female.—A little larger than the male and with the same dermal characters, except that the sharp-pointed papillæ are more developed.

Mandibles: 2 mm. in length.
Palp: the length of the segments is as follows:—

Segment ...	1	2	3	4	5
Length.. ...	240 μ	255 μ	310 μ	125 μ	55 μ

Epimera: similar to those of the male.
Genital area (text-fig. 4): smaller than in the male (length 330 μ, breadth 375 μ).

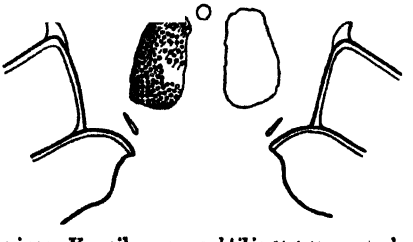
Text-figure 4.



Hydrarachna spinosa Koenike, var. *subtilis* var. n., ♀. Genital area.

The plates are separated by a deep depression anteriorly to about the middle of their length. The greater part of the plates is covered with acetabula, but none of these contain hairs. At the posterior margin of the genital plate, on either side, is a larger and more rounded acetabulum, with a patch of long hairs lateral to it. Isolated hairs are also found between the smaller acetabula.

Text-figure 5.



Hydrarachna spinosa Koenike, var. *subtilis* var. n., nymph. Genital area.

Anus: provided with a chitinous ring; much further from the genital plate than in the male (450 μ).

Nymph.—Length of body 2·1 mm. The structure is very similar to the adult until the genital region (text-fig. 5) is reached. The backwardly-directed prolongation of the third epimeron is, however, separate, lying obliquely in the soft skin, and is not joined to the epimeron as it is in the adult. The genital region is

very different. The plates are separated for a distance of 100 μ at the narrowest point, which is posterior. They are rectangular in shape, rounded behind, with numerous small acetabula between which, over the posterior two-thirds of the plates, are short hairs. The plates do not touch the epimera. In the median line, at the level of the posterior margin of the genital plates, is a chitinous disc for the attachment of a muscle. The anus lies 350 μ behind the median plate and is surrounded by a chitinous ring.

HYDRARACHNA ELDORETICA Lundblad.

Locality.—Wouramboulchi, Serpent Lake, 9000 ft., 3rd Oct., 1 nymph.

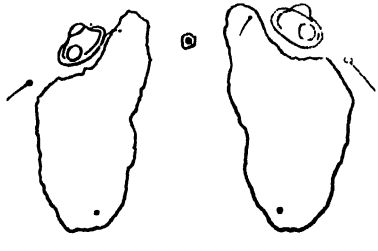
Geographical Distribution.—East Africa: Lake N. of Eldoret in the Mt. Elgon region.

Remarks.—The single specimen appears to belong to the species described by Lundblad, 1927, from the Mt. Elgon region, British East Africa. It differs in a number of minor characters from the type, but this may be due to the fact that Lundblad's description was drawn up from the study of a nymphoderma; all the differences seem to me to be accounted for by the difference in the developmental stage reached by the specimens.

Description.

Nymph.—Body oval; 1·5 mm. long, 1·260 mm. broad. The frontal margin is slightly convex between the antenniform setæ. The upper surface is covered with round papillæ, and there are no sharp papillæ such as are described in the typical nymph. The anterior dorsal plates (text-fig. 6) are also a little longer, being

Text-figure 6.



Hydrarachna eldoretica Lundblad, nymph. Dorsal plates.

465 μ in length with a breadth of 240 μ. Each plate has at its anterior margin beside the eye-capsule, and at the posterior margin a fine hair not shown in Lundblad's fig. 1. The two scales are separated medianly by a wide space.

Capitulum: similar in size and shape to that of the type.

Palp: differs noticeably from the type. The dimensions of the segments are as follows:—

Segment	1	2	3	4	5
Length of extensor side ...	109 μ	123 μ	140 μ	78 μ	36 μ
Length of flexor side	93 μ	70 μ	73 μ	31 μ	23 μ

The total length of the basal segment is 153 μ. The extreme shortness of the third segment is especially noticeable. There are also differences in the number and disposition of the setæ: besides the setæ shown by Lundblad (fig. 3) there is a short strong seta on the outer margin of the second segment and a weak hair near the base of the third segment.

Epimera: as in the type, except only that the fourth plate seems somewhat wider and more rounded externally.

Genital area: the position of the genital plates is similar to that in the type, but they are somewhat narrower in the latter. They also differ in having no large acetabulum near the inner margin, and in having on the anterior half of the plates a spot covered with a few setæ.

LIMNESIA RUGOSA, sp. n.

Locality.—Wouramboulchi, Serpent Lake and marshes, 9000 ft., 2nd–5th Oct., 62 ♀, some young and some mature with eggs, 1 nymph just moulted and unfit for description.

Remarks.—*Limnesia scutellata* Koenike, 1898, is a closely-related form, rather imperfectly described by Koenike, 1898. A direct comparison of the Abyssinian specimens with Koenike's types could not be made, as the latter are not in the Senckenberg Museum. The differences, however, are of such an order that the Abyssinian species must be separated under a new specific name.

Description.

Ripe females have a length of more than 1·5 mm. The following description refers to such mature specimens unless otherwise stated.

Text-figure 7.



Limnesia rugosa, sp. n., ♀. Mandible

Text-figure 8.



Limnesia rugosa, sp. n., ♀. Palp.

Form: broadly oval. Koenike says that there is a tendency to form a plate in *L. scutellata*, and makes no mention of chitinous papillæ on the skin. In *L. rugosa* there is a posterior dorsal plate, rounded but varying somewhat in shape, and having a diameter of 135 μ. The skin also is covered densely with small, sharp,

chitinous papillæ which are difficult to observe, looking from above, especially when the skin is wetted, but can be clearly seen at the edges of the body.

Capitulum : very similar to that of *L. scutellata* Koenike.

Mandible (text-fig. 7): total length 435 μ, almost twice as long as that of the male *L. scutellata*. There is no knee-shaped projection at the basal joint, and the highest point of the mandible (85 μ) lies directly behind the insertion of the claw, which is itself 105 μ in length, strongly curved, and becoming much sharper distally.

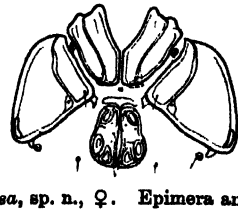
Palp (text-fig. 8): the dimensions of the segments along the extensor side are as follows :—

Segment ...	1	2	3	4	5
Length.....	20 μ	150 μ	115 μ	180 μ	60 μ

There are considerable differences in the palp of *L. scutellata* as figured by Koenike, 1898, fig. 110. In this figure the second and third segments are shown of almost equal length, while in the new species there is a well-marked elongation of the second segment. In Koenike's figure the fourth segment is also relatively shorter, and more curved on the flexor side. In *L. rugosa* the flexor side of the second segment is straight, with a backwardly-directed spine arising some distance behind the margin and not inserted vertically on a swelling as appears to be the case in *L. scutellata* from the rather indistinct drawing. The setæ of *L. rugosa* also appear to be stouter, and particularly noticeable are two long hairs, one on each side of the third segment. One of the tactile hairs of the fourth segment is much longer than the other.

Epimera (text-fig. 9): these are very similar in the two species, the third

Text-figure 9.



Limnesia rugosa, sp. n., ♀. Epimera and genital area.

epimeron forming a right angle (Koenike says "innen nicht eckig"). The "subcutane Fortsatz in fussartiger Form" mentioned by Koenike is present in the Abyssinian form, but the suture lying between the third and fourth plates, being strong, reaches the inner margin of the group of plates, and the inner margin of the fourth epimeron, which bears a glandular pore, is indistinct. The first pair of epimera have their edges parallel internally for about three-sevenths of their length. The total length of the epimeral region is about 600 μ and the breadth 900 μ. In younger specimens it is correspondingly smaller.

Legs : have the following dimensions :—

Leg	1	2	3	4
Length	720 μ	1085 μ	1050 μ	1500 μ

The five or six setæ of the sixth segment of the posterior legs do not stick to the leg, and are feathered like the short setæ of the fourth leg. The longer dagger seta of the apical joint, which is without a claw, is also absent. The wide dagger setæ, mentioned by Koenike as occurring on the third leg of *L. scutellata*,

are absent. Instead of the stout setæ of medium length on the underside of the main segments of the first two pairs of legs, there is on the basal segment of the first leg a short seta, and on that of the second leg a somewhat longer seta.

Genital area (text-fig. 9): even in immature specimens the plates are much longer and wider than in *L. scutellata*—250 μ long, 190 μ broad. In adult females they may reach a length of 275 μ and a breadth of 245 μ. With the growth of the animal the distance between the two plates becomes greater in the posterior half of their length. The middle acetabulum lies for half its length along the outer side of the posterior acetabulum, so that the distance between it and the anterior acetabulum is greater than in the species taken for comparison. The anterior supporting body also shows greater development.

Egg: diameter 180 μ.

PIONA ANGULATA Viets.

Locality.—Djem Djem Forest, pond no. 2, 8100 ft., 26th Sept., 8 ♀ ♀.

Geographical Distribution.—East Africa: Elanairobi crater-lake; West Maiani Steppe; N.W. Ruanda, Galago Lake; crater-lake at the top of Mt. Elgon; lake N. of Eldoret in the Mt. Elgon region.

Remarks.—The Abyssinian specimens agree well with the type. There are but a few minor deviations—for example, the extensor side of the segments of the palp are a little longer and the height is greater in some cases, as follows:—

Segment ...	1	2	3	4	5
Length	50 μ	260 μ	115 μ	270 μ	80
Height ...	—	135 μ	—	60 μ	—

The apical claws are also well developed, and on both sides of the genital furrow the female has 54 to 56 acetabula, making the lateral extension of the genital area somewhat greater—about 600 μ.

PIONA CRASSIPES, sp. n.

Locality.—Wouramboulchi, Serpent Lake, 9000 ft., 3rd–7th Oct., 15 ♂ ♂, 21 ♀ ♀, 28 nymphs.

Remarks.—The nearest relatives of this new species are *P. uncata*, *P. uncata* var. *controversiosa*, *P. brehmi*, and *P. trisetica*.

Description.

Male.—Oval; 1·35 mm. in length. The skin is very thin and, especially in dry preparations, shows an extremely fine wrinkling of the surface.

Capitulum: of the normal shape but very wide in front (255 μ).

Mandible: total length 335 μ. The basal segment bends nearly at right angles at the base to form a sharp knee. The claw is strong and distinctly curved.

Palp (text-fig. 10): the length of the segments along the extensor edge is as follows:—

Segment ...	1	2	3	4	5
Length.....	60 μ	260 μ	110 μ	300 μ	235 μ

The basal segments are decidedly stouter than those of the anterior pair of legs. The second segment has the flexor side straight; the fourth segment is narrow, very slightly curved, and bears ventrally two teeth of unequal size, each of which has a fine hair at its apex. Anterior to these is the characteristic sign of the imminuta in the shape of a small accessory papillæ, and there is a small, though easily perceived, nterio chitinous tooth. The few setæ are feathered.

Epimera (text-fig. 11): the epimeral region is 645 μ in length. The epimera behind the capitulum have the inner margin widely chitinized. Both the posterior groups are ankylosed medianly, but their median edges can be clearly differentiated; they are more closely approximated posteriorly than anteriorly.

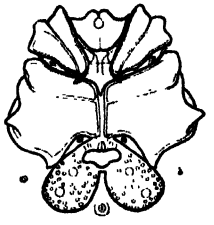
Legs: the three anterior pairs are more slender than the posterior pair. The

Text-figure 10.



Piona crassipes, sp. n., ♂. Palp.

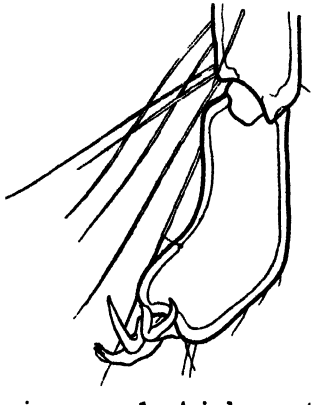
Text-figure 11.



Piona crassipes, sp. n., ♂. Epimera and genital area.

fifth segment of the third pair is sexually modified, serving to convey the sperm, and is 400 μ in length, thickened distally, and bears nine long and several short setæ; the apical segment (text-fig. 12) is 185 μ in length, with the distal curved portion not thickened; the claws are peculiar, one of them having three points. The posterior leg has the two basal segments very stout, with few setæ; its distal grasping-segment is elongated distally and is skittle-shaped, with five swimming-

Text-figure 12.



Piona crassipes, sp. n., ♂. Apical segment of 3rd leg.

hairs; the apical segment is three-quarters of the length of the penultimate segment.

Genital area (text-fig. 11): the plates are large—285 μ long and 495 μ broad. The seminal pouch is widely elliptical, with the posterior margin forming a median bay. On each half of the plate are two large and about forty small acetabula. The excretory pore is at the level of the hinder margin of the plates and is surrounded by a wide chitinous ring.

Female.—Length of body rather more than 2 mm.

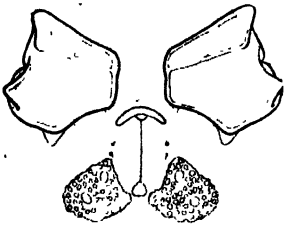
Capitulum : 285 μ wide in front.

Palp : similar to that of the male, but stouter and longer.

Epimera : the first epimeron has the inner margin behind the capitulum narrowly thickened. The gland, as it lies between both groups of epimera of one side, touches the hinder margin of the second plate. The distance between the slightly undulating margins of the posterior groups of epimera medianly is about 200 μ. The posterior projection of the fourth epimeron is short and stout (text-fig. 13).

Genital area (text-fig. 13) : has two large plates, somewhat tongue-shaped, with two large and forty-five to fifty small acetabula. Anterior to each plate are two

Text-figure 13.



Piona crassipes, sp. n., ♀. . Genital area.

setæ surrounded by soft skin. At the posterior corners, opposite the hinder supporting body, are three or four setæ. The genital opening is 300 μ in length, with a strong supporting body in front. The excretory pore lies 200 μ behind the posterior supporting body of the female opening, and is surrounded by a circular chitinous plate.

Nymph.—Length of body 1·2 mm. The young stages are identical with the female even to the genital area. Both genital plates bear two acetabula. They touch each other medianly and are slightly inclined one to the other.

ARRHENURUS PROCERUS, sp. n.

Locality.—Djem Djem Forest, pond no. 2, 8100 ft., 26th Sept., 2 ♀ ♀.

Remarks.—the nearest relative of this new species, of which as yet only females are known, is *A. rudiferus* Koen., from Madagascar and Cameroon.

Description.

Female.—Elongated oval (text-fig. 14), 1·170 mm. in length and ·870 mm. in breadth. The edge of the forehead is vaulted, but the sides of the body are not indented, although in the region of the genital plates the sides are slightly flattened. The dorsal armour is similar in its contours to the general body shape, and is 885 μ in length and 615 μ in breadth ; it reaches more nearly to the posterior margin of the body (75 μ) than to the anterior (195 μ).

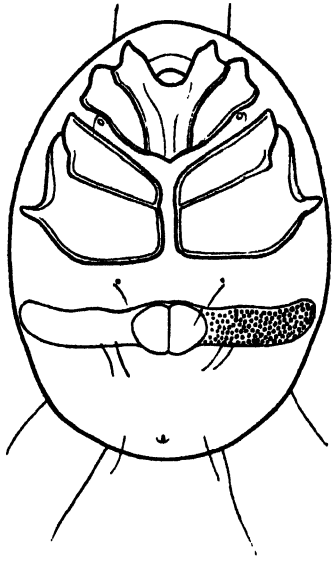
Mandible : 185 μ in length, with the basal region much thinner than in *A. rudiferus*. The flexor side is so slightly curved as to be almost straight. The mandibular hollow is less in circumference and not so deeply excavated as it is in *A. rudiferus*, and the claw is weaker.

Palp (text-fig. 15): the segments, measured along the extensor side, have the following dimensions:—

Segment ...	1	2	3	4	5
Length... ..	35 μ	90 μ	65 μ	95 μ	50 μ

The second segment shows a distinct basal curvature and the fourth segment a break on the extensor side, which causes it to lose thickness distally. The antagonist is directed forwards. The apical joint is inserted far back. The majority of the setæ of the three main segments are feathered.

Text-figure 14.



Arrhenurus procerus, sp. n., ♀. Ventral surface.

Text-figure 15.



Arrhenurus procerus, sp. n., ♀. Palp.

Epimera (text-fig. 14): the epimeral region does not reach to the anterior margin, and the capitular depression is deeper than in *A. rudiferus*. The distance between the posterior groups of epimera is also smaller. The length of the epimeral region is about 600 μ, and it reaches further back than it does in *A. rudiferus*. The inner region of the posterior margin of the fourth epimeron lies transversely, and the posterior angle is hardly indicated.

Genital area (text-fig. 14): lies about 100 μ from the epimera. The lips of the genital opening form an ellipse 155 μ in length and 220 μ in breadth, lying diagonally to the median line; their whole surface is covered with fine pores. The plates are slightly less in diameter than the length of the lips of the genital opening. They lie transversely and extend to the sides of the body, their lateral extremities being curved forwards a little; the anterior margins are undulating and the posterior margins are straight; they are densely covered with small acetabula. The excretory pore lies close to the hind end of the body.

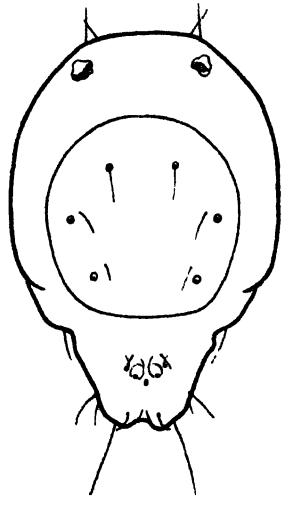
ARRHENURUS INIQUUS, sp. n.

Localities.—Djem Djem Forest, pond no. 2, 8100 ft., 26th Sept., 10 ♀ ♀; Wouramboulchi, Serpent Lake, 9000 ft., 2nd–4th Oct., 2 ♂ ♂, 1 immature ♀.

Description.

Male.—The body, including the appendix (text-fig. 16), has a length of 1·065 mm. and a breadth of ·720 mm. The anterior margin of the body, slanting towards the sides, is straight between the two antenniform setæ, which are 300 μ apart. The sides of the body are almost parallel, but there is a swelling where the body passes into the appendix. The latter is 225 μ in length and at its base is 375 μ in

Text-figure 16.



Arrhenurus iniquus, sp. n., ♂. Dorsal surface.

width and tapers posteriorly. At its hinder end there is a median indentation flanked by small projections, and similar small projections are found at the base of the appendix. The dorsal arch is closed. The dorsal plate is round, with a diameter of 540 μ, and bears three gland pores, the hindermost of which lies upon a low protuberance. The dorsal surface of the appendix is vaulted in the middle and has two pairs of fine hairs in the narrow porous region, while somewhat further back, behind two rounded poreless regions, is a flat depression containing the excretory pore. There is no petiolus.

Capitulum: including the pharynx, which projects behind its posterior margin, the capitulum measures nearly 200 μ.

Mandible: is 200 μ in length and is feeble, with a very feeble claw, especially at its curved end. The basal segment is only slightly thicker proximally than distally.

Palp (text-fig. 17): the length of the segments along the extensor side is as follows:—

Segment ...	1	2	3	4	5
Length	40 μ	95 μ	60 μ	120 μ	50 μ

On its inner side the second segment has three or four fine hairs and a strong feathered seta. The fourth segment is slightly curved and is the same thickness throughout its length, with the antagonist corner rounded and a little extended anteriorly.

Epimera: the length of the epimeral region is 615 μ and its width, at the insertion of the posterior legs, is 800 μ. The median edges of the hind group of epimera are slightly projecting and separated by a distance of 60–70 μ. The posterior margins of the fourth pair of plates are feebly developed.

Text-figure 17.



Arrhenurus iniquus, sp. n., ♂. Palp.

Legs: the three anterior pairs are slender. The posterior legs are strong, with the fourth segment widened distally, 270 μ in length, and not forming a spur, but with the outer edge projecting beyond the insertion of the fifth segment. The numerous setæ of the fourth segment are thin, feathered, and of short or medium length. The penultimate segment is only 225 μ long, is widened distally, and has both a row of swimming-setæ and of medium-length hairs. The terminal segment is 290 μ in length, with the edges extending beyond the base of the claws. The second segment has a row of eight very long swimming-setæ, besides hairs of medium length.

Genital area: this is situated at the region where the body merges into the appendix. The plates, separated by a slit about 60 μ in length, are about 60 μ wide throughout their length and reach to the sides of the body, where they form the strong swellings anterior to the base of the appendix.

Female.—The body (text-fig. 18) is broadly oval, regularly rounded, and but slightly flattened, with a length of 1·155 mm. and a breadth of ·950 mm. The anterior margin, between the two antenniform setæ, is straight. The dorsal armour is ·9 mm. in length and ·660 mm. in breadth, elongated oval in shape, and extending to within 210 μ of the anterior margin and to within 90 μ of the posterior margin of the body.

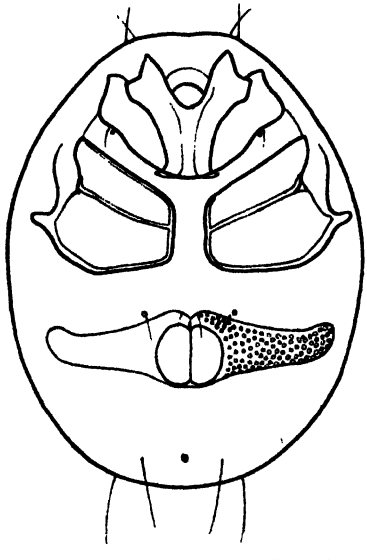
Capitulum and mandible : as in the male.

Palp: the segments are slightly longer than in the male, and the antagonist corner is rather more expanded anteriorly.

Epimera (text-fig. 18): the epimeral region is only 540 μ in length. The third and fourth pairs internally are of about equal dimensions. The posterior groups are separated by a distance of about 90 μ. The hinder margins of the fourth pair for the median half of their length are transverse.

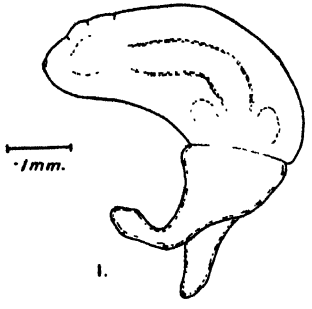
Legs : all four pairs are slender.

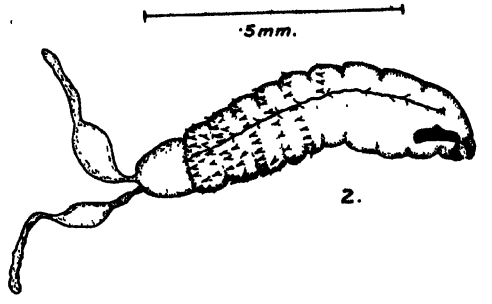
Text-figure 18.

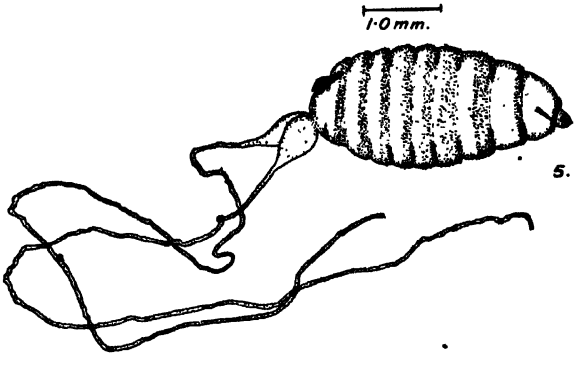


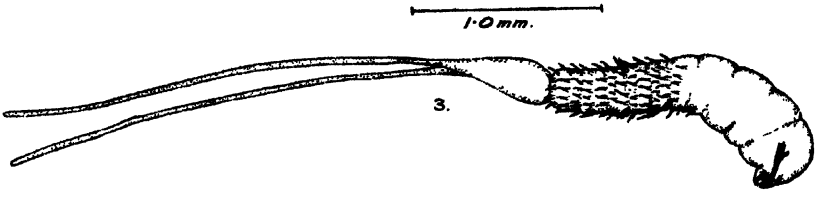
Arrhenurus iniquus, sp. n., ♀. Ventral surface.

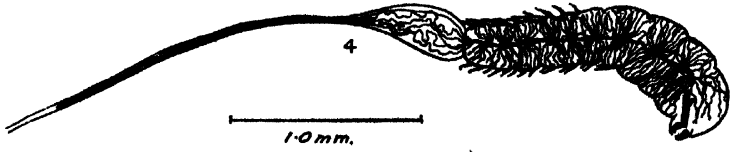
Genital area: lies about 110 μ behind the epimera. The lips without chitinous spots but finely porous, 175 μ long and 190 μ wide, and together are almost circular. The genital plates surround the lips anteriorly, are considerably broader medianly than laterally, and lie transversely, with the outer ends curving forwards. They are densely covered with acetabula which are smaller than the pores of the dorsal armour. The post-epimeral pores are close to the anterior margin of the genital plates. The excretory pore is not far from the hinder end of the body.





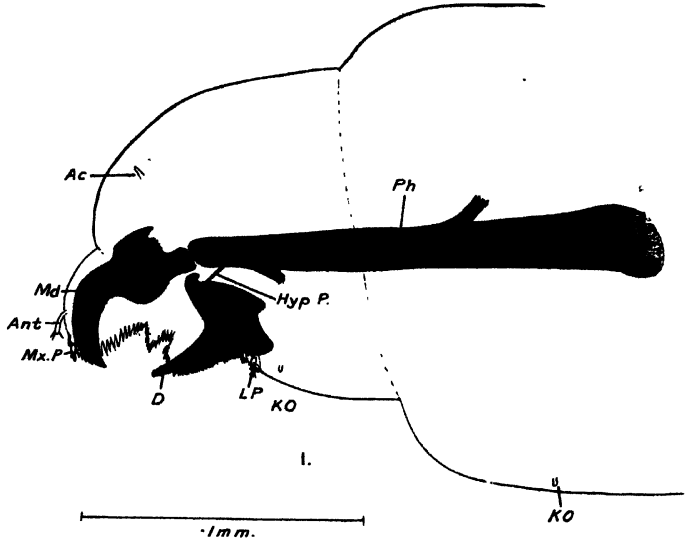


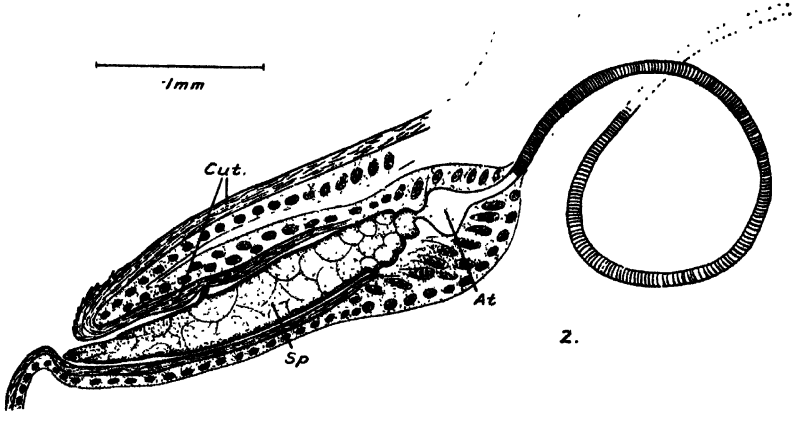


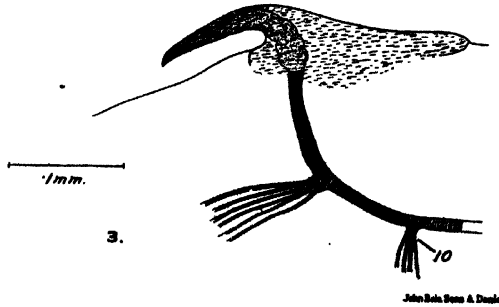


John Bale Sons & Danielsson, Ltd. London

ETC., OF *CRYPTOCHÆTUM ICERYÆ* WILL.



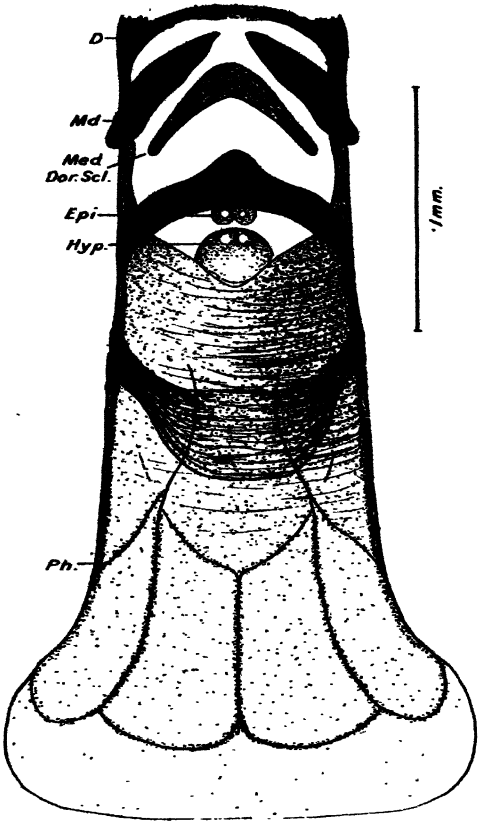




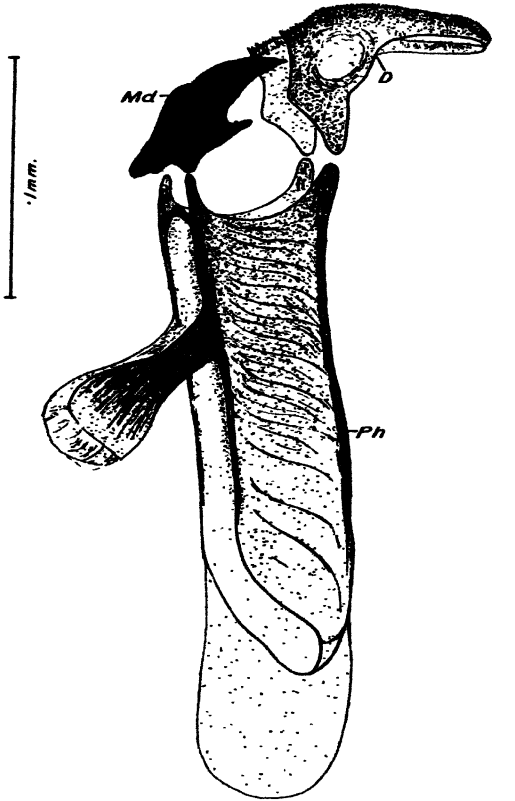
W.H.T. del

John Bale Sons & Danielsson, Ltd. London.

THE BIOLOGY, ETC., OF *CRYPTOCHÆTUM ICERYÆ* WILL.



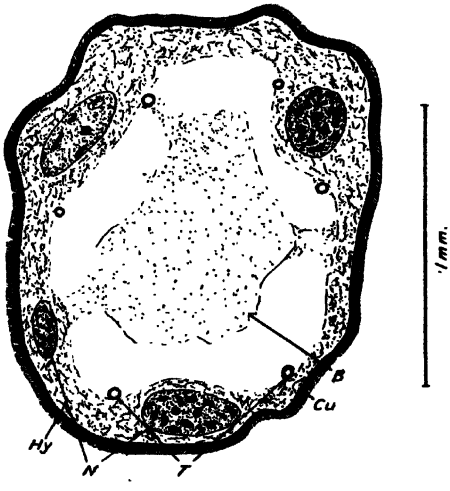
1.



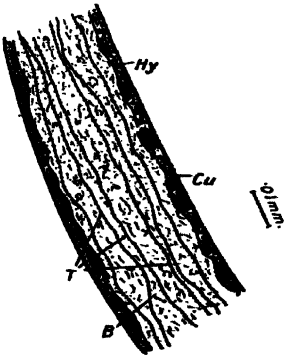
2.

W.H.T. del

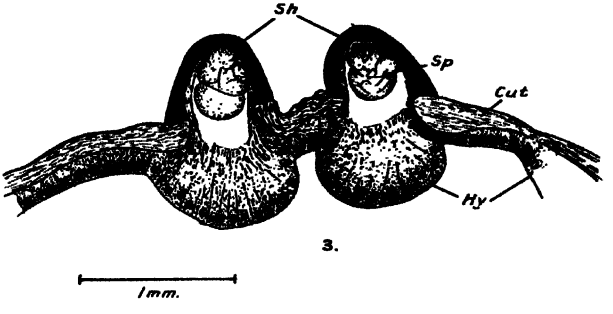
THE BIOLOGY, ETC., OF *CRYPTOCHÆTUM ICERYÆ* WILL.



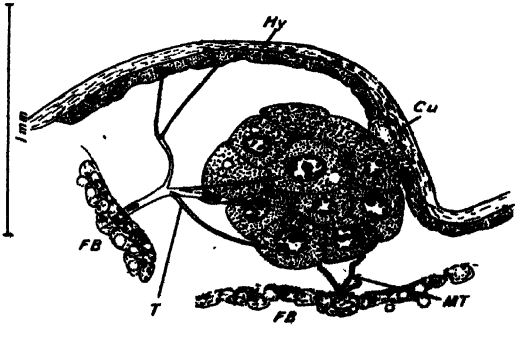
1.



2.



3.

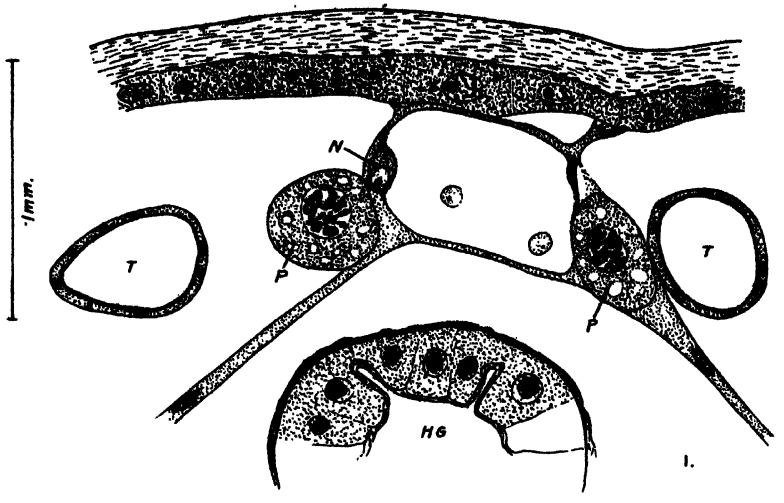


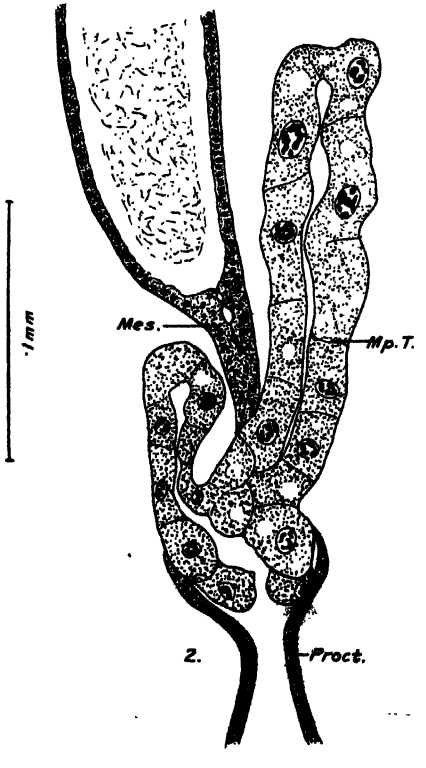
4.

W H T del

John Bale Sons & Danielsson, Ltd London.

THE BIOLOGY, ETC., OF *CRYPTOCHÆTUM ICERYÆ* WILL.





W.H.T. del.

John Bale, Sons & Danielsson, Ltd. London.

THE BIOLOGY, ETC., OF *CRYPTOCHÆTUM ICERYÆ* WILL.

44. The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* (Diptera, Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini).

By W. H. Thorpe, M.A., Ph.D., C.M.Z.S.*

[Received May 17, 1930 : Read October 21, 1930.]

(Plates I.–V.† ; Text-figures 1–23.)

Contents.

	Page
Introduction	929
Methods	930
The Genus *Cryptochætum*	930
The Structure of the Antenna	933
C. iceryæ and its Distinction from closely allied Species	933
Key to the Species	935
History and Economic Importance of *Cryptochætum* in U.S.A.	936
Parasites of *Cryptochætum*	938
Habits of Imago	938
Egg	939
First Stage Larva	940
Second Stage Larva	941
Third Stage Larva	943
External Features	943
Sense Organs	944
Bucco-pharyngeal Apparatus and its Muscles	944
Abdomen	945
Tracheal System	947
Fourth Stage Larva	947
External Features	947
Mouth-parts	948
Spiracles	948
Internal Anatomy	950
Alimentary Canal	950
Malpighian Tubules	951
Salivary Glands	951
Œnocytes	953
Circulatory System	953
Nervous System	954
Habits of Larvæ	954
Puparium	958
Discussion	960
Primary Larva	960
Later Larval Stages	962
Structures characteristic of a Free Life	962
Adaptations to a Parasitic Mode of Life	962
Respiratory Function of Tails	963
Comparison with other Species	967
Summary	968
Bibliography	969
Explanation of the Plates	971

Introduction.

Cryptochætum iceryæ, as is well known, is a native of Australia, and was originally introduced into California in an attempt to control the Cottony Cushion Scale,

* Paper No. 225, Graduate School of Tropical Agriculture and Citrus Experiment Station, University of California, Riverside, California, U.S.A.

† For explanation of the Plates, see p. 971.

Icerya purchasi. It is such a remarkable insect from every point of view that a detailed description of its structure and biology seems desirable. I am indebted to Dr. A. D. Imms, F.R.S., for first drawing my attention to its possibilities as a subject for research.

This study was carried out during the tenure of a Rockefeller Foundation Research Fellowship (1927–29) at the Entomological Department of the University of California Citrus Experiment Station at Riverside, in Southern California, and was completed at the Zoological Laboratory, Cambridge, England,

It is a great pleasure to acknowledge my indebtedness to Professor Harry S. Smith, of the University of California, for the hospitality of his Department, for the laboratory and other facilities so freely given, and, above all, for his interest in the work and his constant readiness to give me the benefit of his very extensive knowledge of parasitic insects.

In connection with the systematic side of the work, I must thank Dr. A. H. Sturtevant, of the California Institute of Technology, Pasadena, for allowing me to examine his collection, and Dr. J. M. Aldrich for permitting me to examine the material in the United States National Museum at Washington. Professor F. Silvestri, of Portici, Italy, also very kindly sent me fresh material of *C. grandicorne*.

Methods.

The host scale was reared, both out of doors and in the greenhouse, on potted citrus trees enclosed in cages of about 12 cu. ft. capacity, with three sides and the top of muslin and the front of glass. It was found impossible to secure normal behaviour of the parasites in smaller cages. The material was obtained from Riverside, Redlands, and Santa Barbara in S. California, and also from the San Francisco Bay region.

For the anatomical study three fixatives were used—Carnoy, Gilson, and Bouin Of these Bouin's alcoholic picro-formol was found the most satisfactory, the greatest difficulty being to secure adequate penetration. Single paraffin embedding after cedar-wood oil was found satisfactory provided a really sharp knife was used.

For the study of living early-stage larvæ methylene blue was employed. For mounting whole unstained larvæ De Faure's Fluid, containing chlorhydrate of cocaine, was excellent. Euparal was useless on account of the distortion it caused. For staining sections ½ per cent. Heidenhain's Iron Hæmatoxylin, Delafield's Hæmatoxylin with Eosin, and Mann's Methylene Blue-Eosin were employed with success, and occasionally Safranin and acid Fuchsin.

The Genus Cryptochætum (Rond.).

The genus *Cryptochætum* was established by Rondani in 1875 to accommodate a very aberrant parasitic fly apparently referable to the family Agromyzidæ. This insect, *C. grandicorne*, is a parasite on the Monophlebine Scale, *Guerinia serratulæ* Fab., in S. Europe. The most striking character is the complete absence of an arista, but the fly is aberrant in many other respects.

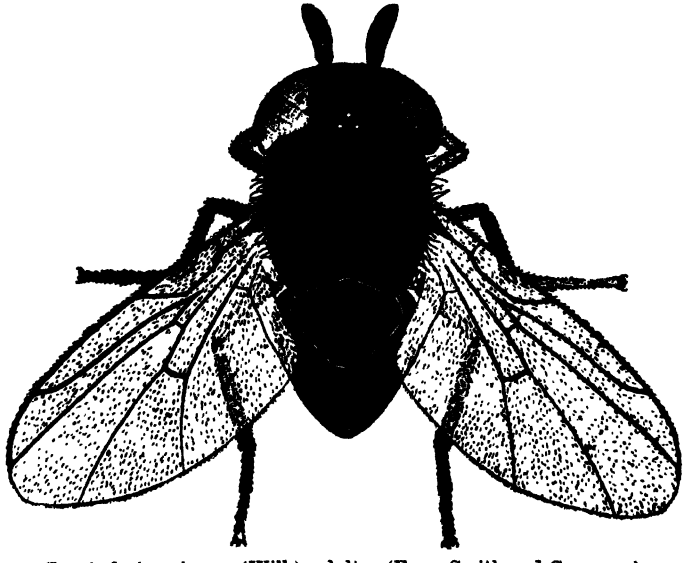
The following is a definition of the genus as it stands at present, slightly modified from Melander (1913):—

Arista completely wanting, third antennal segment large; frons shining and closely hairy, no fronto-orbital bristles or oral vibrissæ; eyes large, cheeks linear; mesonotum hairy, bristleless; no sterno-pleurals, mesopleuræ setulose; scutellum large, triangular, with sharp edge and two minute apical bristles; legs without spurs or bristles; calypter rudimentary, not ciliate; wings short and broad; costa twice broken, extending to R_{4+5}. Cells M_1 and 1st M_2 fused. Subcosta barely distinguishable, parallel to R_1.

The genus is included among the *Agromyzinæ* by both Aldrich and Melander, although this is admittedly a matter of convenience. It has also been referred to

the Oscinidæ and the *Octhiphilinæ*, and there is as much to be said for its inclusion in the *Milichiinæ*, where it is placed by De Meijere (1918). In fact it is so isolated, both structurally and biologically, that it is anomalous in any of the

Text-figure 1.



Cryptochætum iceryæ (Will.), adult. (From Smith and Compere.)

existing groups, and the only logical course would seem to be to make it the type of a new subfamily.

Up to the present time eight species have been described as belonging to this genus, although it seems doubtful whether some of these will stand under further investigation. They are as follows :—

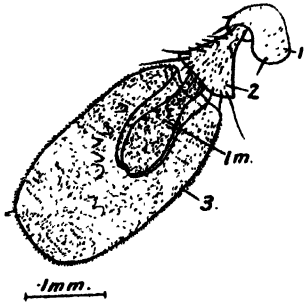
Species.	Host.	Region.
C. iceryæ (Will.)	*Icerya purchasi* (Riley).	Australia. (Introduced California and Florida.)
	Dactylopius sp. (?).	Australia.
C. monophlebi (Skuse)	*Monophlebus crawfordi* (Mask).	Australia.
	Icerya purchasi.	Australia.
	Dactylopius sp. (?)	Australia.
C. chalybeum (De Meij.) ..		Java.
C. curtipenne (Knab)	(*Walkeriana* sp.) *Aspidoproctus cinerea* Green.	Ceylon.
C. latimana (Malloch)		Australia.
C. senescens (De Meij.) . ..	. ..	Java.
C. grandicorne (Rond) . ..	*Guerinia* (*Gueriniella*, *Monophlebus*) *serratulæ* (Fab.).	Italy, N. Africa.
	Icerya seychellarum (Westw.).	Japan.
	Warajicoccus (*Drosicha*) *corpulentus* (Kuwana).	Japan.
C. fastidiosum (Bezzi)		Philippines.

Thus of these eight species, three are native to the Australian region, four have been described from S. and S.E. Asia and the East Indies, while one—*C. grandicorne*—is native to S. Europe, with doubtful records from Formosa and Japan.

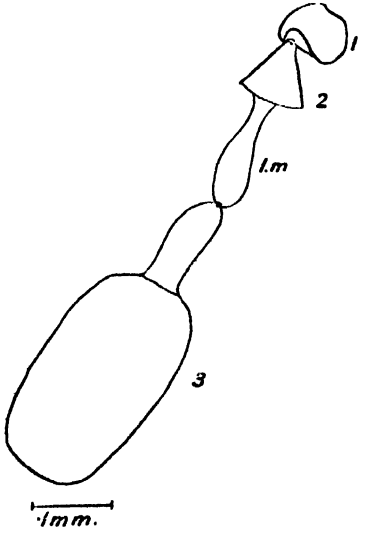
As far as is known, they are parasitic in the early stages on coccids of the subfamily *Monophlebinæ*.

Lefroy describes a member of this genus as being a very annoying eye-fly in the jungle at Pusa, S. India. There is a similar record quoted by Bezzi for

Text-figure 2.



Text-figure 3.



Text-figure 4.

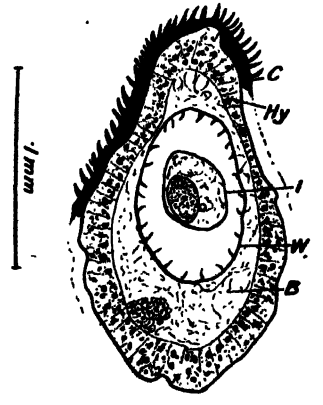


Fig. 2.—Antenna, cleared in xylol, showing true structure of third segment. *I.m.* Intersegmental membranous part.

Fig. 3.—Antenna, cleared in xylol, showing lining of pit and third segment accidentally everted after boiling in potash.

Fig. 4.—Antenna (*C. grandicorne*). Transverse section through third segment. *B.* Blood-space. *C.* Chitinous cuticle of third segment. *Hy.* Hypodermis. *I.* Inter-segmental club-shaped piece showing trachea and nerve. *W.* Inner wall of third segment.

C. fastidiosum in the Philippines, so there can hardly be any doubt about the matter. Nevertheless it is an extraordinary habit for a parasitic insect, and further details are much to be desired. It is noteworthy that a similar habit is prevalent among several of the closely allied family Chloropidæ.

The species to which Lefroy refers was not identified, and nothing is known of its life-history save that "the adult is often found sitting on stems or leaves or in crevices of tree-trunks in small groups of half-a dozen or so individuals." He also remarks that it will live longer in a corked tube than any other fly he has ever observed, a characteristic in very great contrast to *C. iceryæ*, which is so delicate and intolerant of confinement.

The Structure of the Antenna.

Sturtevant (1925–6) has questioned the absence of the arista, suggesting that what appears to be the third segment is in reality a huge arista shaped like the cover of a book, and completely enfolding the true third segment. With this conclusion I am unable to agree. Sections of the antenna (text-fig. 4) show the true state of affairs. The conspicuous terminal segment is, as it appears to be, the true third segment. It is, however, affixed to the second segment in a very curious way. The point of attachment is sunk into a deep pit, and the intersegmental membranous part is enlarged to form a club shaped structure which nearly fills this cavity. That this club-shaped structure is really intersegmental, and not the true third segment, is shown (text-figs. 2–4) by the absence of cuticular spines; all the true segments have these highly developed. The whole apparatus is, as far as I know, quite unique, and an explanation of it is wanting. The spine on the terminal segment is, of course, not an arista, but equivalent to the antennal spine found, in allied genera, in addition to a true arista.

The Distinction of Cryptochætum iceryæ *from closely Allied Species.*

CRYPTOCHÆTUM ICERYÆ (Will.).

(*Lestophonus iceryæ* Will., *Cryptochætum monophlebi* Knab, *Cryptochætum monophlebi* Smith & Compere.)

Small bluish-black flies with a metallic lustre; abdomen usually more shining, with a greenish tinge; antennæ blackish; legs black, with lighter coloured tarsi; wings short and broad, hyaline, with metallic purplish reflections; veins dark brown; length, av. 1·5 mm., although size may vary greatly according to the size of host and the number of larvæ per host.

Head.—Frons broad, with apex blunt, almost as wide as the distance between antennæ; orbital triangles opaque and somewhat variable in size; post-verticals undifferentiated. Eyes large, bright red, with microscopic black hairs. Antennæ with first and second segments small; third segment large, rounded in outline or with a very weak angulation, covered with a dense brown pubescence and bearing a minute apical spine.

Thorax.—Mesonotum closely hairy, without bristles. Scutellum large, triangular, with a sharp edge and two apical bristles, but slightly differentiated from the close set hairs.

Wings short. R_1 distinctly angulate; course of subcosta indicated by a very pale line, barely distinguishable, and running parallel to R_1 throughout its entire length; the costa twice broken; R_{2+3} and R_{4+5} usually divergent, R_{4+5} ending typically slightly before the apex of wing. Median cell and 1st M_2 fused. *R.M.c.v.* slightly proximal to end of R_1. *M.C.c.v.* arcuate, convexity towards 2nd M_2.

Legs black. Tarsi yellowish brown, with a longitudinal series of short black hairs; no spurs or bristles.

There has been much confusion as to the identity of the species of *Cryptochætum* (*Lestophonus*) introduced into California, owing partly to unfortunate errors in the figure published with Williston's first description (1888). This figure, which is totally incorrect as regards the venation, was corrected by Williston himself later in the same year; but, unfortunately, has been reproduced by Essig in 'Insects of Western North America,' p. 615. In 1889 Skuse, who had been misled by

Williston's first figure, redescribed the species with a correct drawing, and added a new species, *Lestophonus monophlebi*, confined to *Monophlebus crawfordi* (Mask.) in Australia, *iceryæ* being reared both from *M. crawfordi* and *Icerya purchasi* (Mask.). In the same year Mik showed that *Lestophonus* was congeneric with *Cryptochætum*, established by Rondani in 1875 for the European species *grandicorne*. Nothing more was published till 1914, when Knab undertook to determine the identity of the species then found to be widespread in California. Knab published a revision of the genus, in which, through either typographical or other error, and in part due to Williston's incorrect figure, he reversed the most important diagnostic characters of Skuse's two species, describing the one then common as *C. monophlebi*, and expressing a doubt whether the other was ever established. Following him, Smith and Compere (1916) thus described the one occurring in California as *monophlebi*. Essig (1922), at the suggestion of Aldrich, restored the name *iceryæ*, regarding *monophlebi* as a synonym.

Owing to this confusion, the best course seemed to be to examine all available material following Skuse's original description, and completely ignoring Knab's revision, the errors of which merely make confusion worse confounded. Besides a large number of specimens of my own rearing, the collections of the U.S. National Museum, the Citrus Experiment Station, the Philadelphia Academy of Sciences, and of Mr. P. H. Timberlake and Dr. A. H. Sturtevant were examined in this way.

As a result of the investigation it can be said that, although the species is somewhat variable, all but three of the specimens from California agree with *C. iceryæ* Skuse as opposed to *C. monophlebi*. The three *monophlebi* are specimens sent by Coquillet from Los Angeles to Washington in 1888 or 1889. There are also in the National Museum some 50 specimens of *monophlebi* Skuse, all collected in Australia by Crawford and Koebele, with breeding records from *Icerya* and *Monophlebus*.

It seems, therefore, that both species were introduced, but that only one, *C. iceryæ*, was successfully established, the favourite host of the other being absent. In this connection it is interesting to note that, according to Howard (Ins. Life, i. p. 328), most of the material for introduction was obtained from *Monophlebus*, as this was the more prevalent of the two in Australia, and this fact may account for the apparent lack of success and slow rate of spread of the insect when first introduced, for in all probability only a very few *iceryæ* were liberated.

Of the various slight differences which have been put forward as satisfactory specific characters, the following are the only ones which I have found to be sufficiently definite and constant for distinguishing *iceryæ* from *monophlebi*.

In *iceryæ* (Will.) the wings are short and broad; R_1 (1st longitudinal) is distinctly angulated; the radio-medial cross-vein is placed slightly proximal to the end of R_1, and the third antennal segment is usually rounded in outline and bears a minute apical spine.

In *monophlebi* (Skuse) the wings are somewhat narrow and longer; R_1 is definitely curved and not angulated; the radio-medial cross-vein is placed level with or beyond the end of R_1, and the third antennal segment bears a minute apical tubercle and is often markedly angulate.

It will be seen that these few characters which are constant are, nevertheless, very trivial, and the available evidence suggests that possibly *monophlebi* and *iceryæ* would be more correctly regarded as two biological races adapted to different hosts. This point could, of course, only be settled by careful biological work carried out by some worker suitably situated in Australia. Possibly a study of the larval stages of *C. monophlebi* might reveal something more tangible, and experiments on the host and mating preferences of the two forms should also be undertaken.

There has also been some confusion over the separation of *C. iceryæ* and *C. grandicorne* which it seems well to straighten out at this point.

Through the kindness of Prof. F. Silvestri I was able to examine a number of living specimens of the latter species reared from *Guerinia serratulæ* in Italy, and apart from the slightly larger size, which is not a reliable character, found it easily separable from *C. iceryæ* by the following characters:—

Frons small, sharply pointed. Eyes bare, dull brownish red. Antennal spine very minute, hardly distinguishable from the surrounding hairs. Wings dusted with white. (This last character, which is the most obvious difference in the living insects, is not reliable in preserved specimens.)

Kuwana (1922) records a species of *Cryptochætum* as a parasite on *Icerya seychellarum* (Westw.) and *Warajicoccus* (*Drosicha*) *corpulentus* (Kuwana). He sent specimens to Prof. H. S. Smith, who stated that they were definitely not *C. iceryæ* but were close to the European species, and advised they should be sent to Bezzi, which was accordingly done through Prof. Silvestri. Silvestri eventually (Dec. 16th 1918) replied:—"He (Bezzi) thinks that the Japanese specimens are referable to *C. iceryæ* (Will.), which is apparently the same species as *C. grandicorne* (Rond.); at least he does not see any appreciable difference except in colour, which in the Japanese species is a little more metallic." This is an inexplicable verdict when we consider that Bezzi himself in a paper published the following year placed *grandicorne* in a different subgenus from *iceryæ* and *monophlebi*, the frontal triangle being the chief distinguishing character. Bezzi, in the same paper, describes *grandicorne* as confined to S. Europe, throws doubt on the Formosan record, and refers to specimens of *C. iceryæ* * from Japan which he had seen "a mezzo del Professor Silvestri."

I have, unfortunately, not yet been able to obtain material from Japan for study, so that until further evidence is forthcoming we must suppose that the species is *grandicorne*.

That *grandicorne* and *iceryæ* are distinct cannot be doubted now that we have some knowledge of the larval stages, which are quite different.

The following key, including all the known species, has been constructed on what appear to be the most reliable characters, and should aid in the identification of the species. It seems very doubtful if *curtipenne* is really distinct from *monophlebi*. All available material, including the type-specimen, is in such poor condition that it is impossible to come to a definite conclusion. The division by Bezzi into subgenera seems hardly justifiable on such trivial characters. As the genus is a small one it is of no particular utility, and has accordingly been omitted.

Key to the Species.

1. Frontal triangle small, sharply pointed, the point much narrower than the distance between the bases of the antennæ 2.
 Frontal triangle large, occupying almost the entire front, the apex blunt and almost as wide as the distance between the bases of the antennæ 4.
2. Wings slightly infuscated, with the costa extending to the end of M_1. R_{4+5} terminating at the apex of the wing, slightly divergent from M_1. Antennæ a little longer than the face *fastidiosum* (Bezzi).
 Wings hyaline or dusted with white, costa extending to the end of R_{4+5} or a little beyond; antennæ as long as the face 3.
3. Wings hyaline; R_{4+5} terminating at apex of the wing and but a little divergent from M_1; distal portion of Cu_1 but little longer than the posterior cross-vein. Wings and body 3 mm. long... *senescens* (De Meij.).
 Wings dusted with white; R_{4+5} terminating before the apex of wing and strongly divergent from M_1. Distal section of Cu_1 much longer than posterior cross-vein. Wings less than 3 mm. long . .. *grandicorne* (Rondani).
4. Fore tarsi of male strongly dilated *latimana* (Malloch).
 Fore tarsi of male normal 5.

* Bezzi in this paper was following Knab's description, so that his *iceryæ* is really the *monophlebi* of Skuse and his *monophlebi* the *iceryæ* of Williston and Skuse.

5. Radio-medial cross-vein placed slightly proximal to the end of R_1 ...	6.
Radio-medial cross-vein on a level with, or distal to, the end of R_1; R_1 curved, not angulated; 3rd antennal segment with a minute apical tubercle	*monophlebi* (Skuse).
6. Posterior cross-vein straight	7.
Posterior cross-vein curved, sometimes incomplete. R_1 distinctly angulated, 3rd antennal segment with a minute apical spine	*icerya* (Will.).
7. Third antennal segment rounded at apex. Distal section of M_1 normal	*chalybeum* (De Meij.).
Third antennal segment prolonged at the upper angle to a sharp point; distal section of M_1 faint and indistinct	*curtipenne* (Knab).

The History and Economic Importance of *Cryptochætum* in U.S.A.

Credit for the discovery of *Cryptochætum icerya* belongs to F. S. Crawford, of Adelaide, S. Australia, who, at the request of the U.S. Department of Agriculture, sent specimens to the U.S. National Museum in 1888 which were described by Williston the same year, the first introduction to California being made through Crawford vary shortly afterward. The numbers forwarded in this first shipmen do not appear to have been recorded, but they were few, and it is unlikely that any established themselves. In August of the same year A. Koebele was sent to Australia to study the parasites of *Icerya purchasi* in their native country, and as a result of his efforts a further introduction of some 10,000 scale was made in November 1888, of which it was estimated about 50 per cent. were parasitized. With this shipment were included a few specimens of a coccinellid, *Vedalia* (*Rodolia*) *cardinalis*, and of other natural enemies. Efforts were made to propagate these on heavily-infested caged trees in Los Angeles Co. In May 1889 it was reported that, while the *Vedalia* was reproducing very rapidly, and were giving great promise of control, the "Lestophonus" was only developing very slowly. The following month another shipment of 12,000 parasites was made, very few of which came through successfully, and in April 1889 Koebele sent a final consignment before himself returning to the United States. In June Coquillet (1889) reported almost complete lack of success in colonizing *Lestophonus* whereas the *Vedalia* was reported to be flourishing exceedingly.

The probable reason for this difficulty is establishing *Cryptochætum*, and for its very slow rate of spread, has been suggested above.

The story of the astonishing success of *Vedalia*, and how it saved the fortunes of the Citrus industry in California, is too well known to need repetition here. The result, however, was that no further attention was given to *Cryptochætum*, although Riley expressed the opinion that its importance was not yet appreciated; consequently it remained untouched, although it possesses what is, perhaps, one of the most remarkable larval forms in the whole of the Diptera. In fact there does not seem to have been any reference to it in the literature for the ensuing 20 years (1890–1911). In all probability its very existence in California was not definitely known during the greater part of this time.

In 1916 Smith and Compere described it as being found in most of the Citrus sections of South California inhabited by *Icerya*, and credited it with a large share of the work of control, the whole of which had been previously put down to *Vedalia*. As a result of these observations it was introduced into Louisiana and Florida, through Prof. H. S. Smith, in 1917, and artificial propagation was carried out in the latter State during the two succeeding years.

Essig also has pointed out (1926) that in the San Francisco Bay region, where the *Vedalia*, owing to unfavourable winter climate, has long since died out, the scale is kept at a very low numerical status by the activity of *Cryptochætum* alone. In fact from Prof. Essig's account, and from the writer's own experience, it appears that the control attained in this part of the State is very nearly, if not quite, equal to that occurring in regions where *Vedalia* is abundant. There

seems no doubt that either of these natural enemies alone is quite capable of giving a satisfactory control of *Icerya*.

There are, unfortunately, not sufficient data available to give anything like a reliable figure for the average percentage of parasitism over the whole State, and, moreover, percentage of parasitism means nothing taken by itself. It would seem safe to say that in the North it must amount to at least 60 per cent. In Southern California the average is certainly a good deal lower, perhaps owing to the action of *Vedalia*. Nevertheless even here the insect is of very real value, and in the case of isolated infestations not yet discovered by the *Vedalia* a parasitism of 90 per cent. is by no means unusual, the infestation in such cases being very quickly wiped out. Smith and Compere record that as far as their observations go the parasite is more abundant in scales infesting Acacia trees than in those on Citrus. This may well be, for it has been shown in more than one instance among parasitic Hymenoptera—notably in the case of the chalcid *Encarsia parthenopea* parasitic on *Trialeurodes vaporariorum* (Speyer, 1929)—that some host-plants exercise a powerful repellent effect resulting in a much lower percentage of parasitism. The *Icerya* is now so much reduced that I was unable to find enough natural infestations to provide any further evidence in this matter.

Since *Vedalia* constitutes, perhaps, the outstanding case of biological control it is interesting to find that there is another insect enemy which is also capable, at any rate under certain conditions, of keeping the scale in check satisfactorily. Such cases are so rare, when we consider the large number of attempts the world over, that it is worth considering whether there may not be some common factor or set of factors which makes for success in the two cases.

The success of *Vedalia* is usually put down to seven main reasons :—

(1) It is largely independent of climatic conditions ; almost everywhere that the host can flourish so can the coccinellid.

(2) *Vedalia* is a specific predator, a most valuable type, in that each insect attacks many individuals of its prey, destroying each, and thus at once preventing further damage, but at the same time confining itself to one species.

(3) *Vedalia* attacks all stages, from egg to adult.

(4) The coccinellid is very active and spreads rapidly, while the prey is sedentary.

(5) It has, roughly, three generations to one of its prey.

(6) It is exceptionally free from natural enemies.

(7) Finally the scale is not prolific as scales go ; moreover, it is large, and not hidden away in crannies as are many smaller scales, with the result that it is easily located by its natural enemies.

With a moment's reflection it will be seen that, with the exception of (2) and (3), these also apply to *Cryptochætum*. In the first place it seems, if anything, more tolerant of low temperatures than *Vedalia*. True, it is at a disadvantage in that each individual parasite only destroys a single host, but it is absolutely specific to one species of host, and the scale is nearly always destroyed before the reproductive stage has been attained.

With regard to the third point, *Cryptochætum* is definitely at a disadvantage, and on (4) the two are about equal. On the fifth count *Cryptochætum* is about equal to *Vedalia*, and also produces about the same number of eggs. Again, *Cryptochætum*, although attacked by secondaries in Australia, was freed from these before introduction, and has so far remained unattacked by parasites in its new environment.

It is true that *Cryptochætum* is at a disadvantage in that a large number of larvæ may develop in a single host, but it must be remembered that under conditions of plenty the parasite larvæ tend to be more thinly spread over the

whole infestation. This, however, really works to its advantage when food becomes scarce, since then a relatively small infestation of the *Icerya* will yield a large number of adult flies capable of spreading widely and seeking out isolated colonies of scale. Under similar conditions but few individuals of *Vedalia* would reach maturity, since each larva requires several hosts in order to complete its development, and the numbers would be so reduced that there would be a serious danger of their being unable to establish themselves on fresh groups of host. It is well known that *Vedalia* is often liable to local extinction in this way, and this difference in life-history of the two insects may be one of the reasons why *Cryptochætum* is often of great value in searching out and controlling isolated batches of scale before *Vedalia* has succeeded in discovering them. *Vedalia* has the advantage in that it seems somewhat more stable and less erratic and temperamental by nature than does *Cryptochætum* which, in common with many other Diptera, is easily upset as to mating behaviour by slight fluctuations in environmental conditions.

Finally, it should be said that the oviposition of *Cryptochætum* is easily interfered with by the various ants, such as *Iridomyrmex* and *Solenopsis*, which often swarm over the coccids, attracted by the honey-dew, whereas *Vedalia* is troubled but little, if at all, in this way.

From these considerations it can be seen that on theoretical grounds we might expect *Cryptochætum* to be almost as successful a natural check as *Vedalia*, a conclusion which is completely borne out in practice.

The Parasites of *Cryptochætum*.

Only two parasites have been recorded on the genus.

Eurysichia lestophoni (How.), an Elasmid, occurs on *C. iceryæ* or *C. monophlebi* in Australia. Although material infected with this parasite was sent over with the original introduction, its establishment in California was fortunately prevented.

Pachyneuron coccorum (L), a Pteromalid, is recorded by Vayssière as a parasite on *C. grandicorne* in Europe. Although there are several species of this genus in California, at least one of which is very common on *Leucopis*, there are as yet no records of it attacking *Cryptochætum*.

The Habits of Imago.

The adult flies move slowly when on the food-plant of their host, stopping now and again to feed on the sugary exudations or "honey-dew" which the scale produces in such abundance, or to investigate one of the hosts. The flight is rapid and erratic, and in the cages is seldom long sustained. Activity is at its greatest in the early morning, and, at any rate in captivity, ceases almost entirely after noon, when the insects will sit perfectly motionless for long periods.

Cryptochætum is intolerant of captivity, and it was found next to impossible to secure normal behaviour in any except large cages. In small tubes and cages they become very restive, and quickly kill themselves by dashing against the glass.

Duration of life in cages was seldom more than three days, although there was always abundance of "honey-dew" for them to feed upon. They will also readily imbibe sweetened water, and, fed in this way, there is one record of ten days (Smith and Compere, 1916). Length of life no doubt depends very largely on temperature, and is almost certainly much greater under natural conditions.

The sexes are found in approximately equal numbers, and although, owing to the difficulty of securing oviposition in small cages, a conclusive test was not carried out, yet there is no suggestion whatever that parthenogenesis takes place.

Copulation was observed fairly frequently, always in the morning, usually before 10 A.M. The male is mounted on the back of the female, with the tip of his

abdomen curved down over hers, presumably a case of male vertical pose with inverse correlation, as seems to be the general rule among Diptera; before breaking away a false linear pose is often assumed. The male genitalia show the usual twist through 360° which is associated with this type of mating.

Oviposition may commence very soon after emergence, newly-emerged flies having well-developed eggs in the oviducts.

When about to lay, the female walks slowly over scales, moving her antennæ slightly, but not, as far as could be seen, actually touching the scale with them. From various observations it seems clear that she is able to distinguish scales which already contain larvæ in the later stages of development, and as a rule avoids these for oviposition unless the cages are very crowed and unparasitised scales scarce. Whether this is merely a perception of slightly altered form—the scales containing older larvæ becoming more convex—or whether some other sense is involved is an interesting question which cannot at present be answered.

It seems fairly certain that most parasites are unable to distinguish unparasitised from parasitised hosts containing freshly-deposited eggs, even in those cases where only a single individual is capable of maturing in each. *Cardiochiles nigriceps*, an ichneumonid parasite of *Heliothis virescens* Fab. (Chamberlin and Tenhet, 1926), appears to be an exception to this, although the evidence is not conclusive. More commonly a female is capable of avoiding hosts in which she herself has previously oviposited although she cannot distinguish parasitised hosts as such, e. g., *Platygaster hiemalis* (Hill, 1925).

In this connection it is interesting to note that, although the scale *Guerinia serratulæ* can never bring to maturity more than one individual of *Cryptochætum grandicorne*, yet one individual female may deposit many eggs in a single host, and several young larvæ may be found together (Vassière, 1926).

Scales which are about half-grown (second instar) are usually chosen for oviposition, and from the nature of the case usually "female" scales—hermaphrodites as they are now known to—are used. It is, however, worth mentioning that in one cage in which a number of males happened to be produced these were used for oviposition, and were later found to contain healthy larvæ.

Oviposition is accomplished very rapidly, the eggs being inserted almost at random in the hæmocœl of the host. Dissections indicate that somewhere about 200 eggs may be laid by a single female*, and it seems probable that occasionally one female will deposit several eggs at a time, for in one or two cases I have found a scale on dissection to contain ten or twelve larvæ all at exactly the same stage of development. One instance was found in which the ovipositor had been plunged in in such a way that the gut was penetrated and an egg deposited within the mesenteron.

The Egg.

The egg (text-fig. 5), which is slightly kidney-shaped, is about ·19 mm. long and ·08 mm. across at the widest part, the smallest example being ·147 × ·075 mm. There is a minute funnel-shaped micropyle at the larger end which easily gets broken off in manipulation, and in one or two cases could not be found. The figure given by Essig (1926) from Williston has been incorrectly labelled, and depicts not the egg, but the third antennal segment of the adult!

According to my observations, the duration of this stage is from three to four days, but Smith and Compere (1916) place it slightly higher—from four to five.

There is, apparently, a very high mortality in this stage, and eggs with the contents brown and shrunken, with a light margin all round, were frequently

* Vayssière, referring to *C. grandicorne*, says: "Je ne pense pas que le nombre d'œufs déposés par une seule femelle soit aussi considérable et dépasse la dizaine." This can hardly be correct, for I have myself dissected a female *grandicorne* which contained upwards of 230 well-developed eggs.

observed. In one case in which counts were made from a natural infestation, dead eggs amounted to nearly 20 per cent. of the total number laid. I was unable to find any particular reason for this, although it is a common and important factor in the natural mortality of many insects. Lack of fertilization may conceivably be the cause.

During development the egg increases very considerably in size, presumably absorbing water and food-material from the body-fluids of the host in which it is

Text-figure 5.



Egg.

bathed, after the manner of the eggs of many parasitic Hymenoptera. Thus the egg nearly ready to hatch may measure as much as ·31 mm. × ·138 mm.

Numerous attempts to observe the different embryonic stages and the emergence of the primary larva by dissecting out freshly-laid eggs and placing them in sterile hanging-drop cultures were failures. Pure host-blood could not be used owing to its rapid coagulation and its opacity, but equal mixtures of blood and ·75 per cent. NaCl, or salt solution alone gave no results.

The First Stage Larva.

The newly-hatched first stage larva (Pl. I. fig. 1) is of a very remarkable type. It is little more than a cylindrical transparent sac ·3–·4 mm. in length and slightly curved ventrally. Some specimens show no trace of segmentation whatever, while others show a mere suggestion of transverse constriction in the anterior region only. Posteriorly the body terminates in a pair of large finger-like diverticula of about ·35 mm., making a total length of ·65–·75 mm. These are simply lobes of the body-wall containing blood, the cavity of each being continuous with the hæmocœl.

The cuticle is extremely thin, and is smooth save for a slight scar at the anterior end, which marks the position of the future mouth-opening. Careful search failed to reveal any sense organs.

Chitinised mouth-parts are lacking, and there is apparently no mouth-opening. Certainly no food is taken into the gut.

The larva is incapable of movement, and cuticular muscles are as yet undeveloped.

The larva is completely apneustic and atracheate, and no trace of heart, heart-beat, or blood circulation could be seen.

The gut is complete, and runs straight from end to end of the body. The fore gut is apparently closed and without an opening into the mid gut, and no salivary glands could be observed. The mid gut is seen to be distended with a clear fluid and shows regular peristaltic contractions—the only movement the larva ever shows. The junction with the hind gut is marked by short stout lobes, which represent the malpighian tubes. The proctodæum is closed, having no through connection with the cavity of the mid gut, but whether an open anus exists could not be determined for certain, although no traces of one could be seen.

One of the most striking features of the larva in this and in later stages is the large size of the nuclei of the hypodermal cells in the tails, which are easily visible even in unstained specimens.

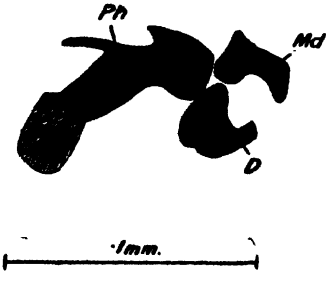
The duration of the first stage could not be determined exactly, but it is very short, being almost certainly not more than two days. During this period growth is rapid, the total length of the larva increasing from about ·7 to ·94 mm.

The Second Stage Larva.

The second stage larva (Pl. I. fig. 2) is about 1·02 mm. long.

The body is curved into a slight S-shape, tapers at both ends, and is now divided into ten fairly distinct segments, the diameter being greatest at numbers 3 and 4. At the anterior end there is now an open mouth with strongly chitinized mouth-parts, which are in constant motion. Sense organs are present, and are similar to those described for the third stage larva. The cuticle is delicate and transparent, and the first four segments are without cuticular processes. The 5th segment bears a few short, pointed, chitinous filaments, chiefly on the dorsal

Text-figure 6.



Second instar larva, mouth-parts. Potash preparation.

D. Dentate sclerite. *Md.* Mandibular sclerite. *Ph.* Pharyngeal sclerite.

side, and each of the remaining segments bears a complete ring of these. Segments 6, 7, and 8 have a single row on the posterior border of the segment, with supernumerary ones on the ventral surface, while segments 9 and 10 have a large number, covering almost the whole surface.

The tails are very variable in shape, and a little less than the body in length. At the base, and sometimes in the middle region, they are distended with blood, as in the first stage, while towards the tips there is no lumen, the tail there consisting of a solid string of hypodermal cells.

Besides the mouth-part muscles, which will be described in connection with the next stage, a certain number of longitudinal segmental muscles are now developed which enable the larva to straighten itself or accentuate the S-curve to a slight degree. This is the only movement ever seen, and transverse segmental muscles are lacking.

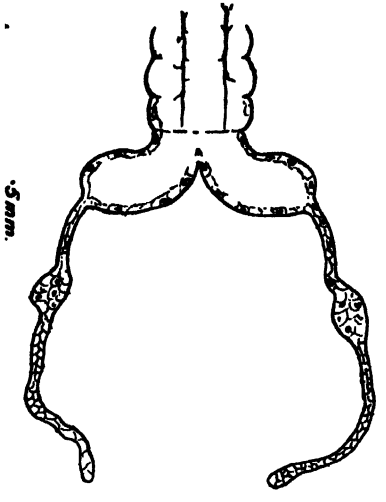
A simple apneustic tracheal system is developed during this stage, and consists of two longitudinal tracheal trunks with little or no branching, extending from segment 1 to the posterior border of segment 10. No transverse commissures are present. In one or two instances no tracheal system could be observed, these presumably being younger larvæ in which the trunks had not yet become filled with gas.

Later in the second larval stage each tracheal trunk sends fine branches, usually

six in number, into the broad open base of each tail, where they lie in somewhat tangled coils.

The mouth-parts (text-fig. 6) are well sclerotised, and consist of a trough-like pharyngeal sclerite, paired mandibular sclerites fused together in the median

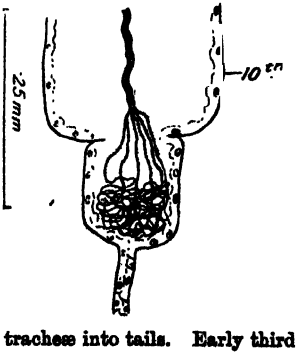
Text-figure 7.



Structure of tails in second instar.

ventral line, and thus working in unison, and a dentate sclerite. The extent of sclerotisation seems rather variable, so that it is often difficult to be certain of the exact shape of the pieces. This is easily understood in view of the fact that these structures are developed during this instar. The figure was drawn after

Text-figure 8.



Entry of trachese into tails. Early third instar.

treatment for a short while with cold, strong, KOH. There is no essential difference in the mode of action of the mouth-apparatus between this and the following stage, which is described in detail.

The mid gut has now increased slightly in length, but the junction of mid and

hind gut is still closed. Salivary glands are now present, but no heart-beat or blood-flow, other than that caused by the movements of the body or gut, could be observed. In general the internal anatomy is closely similar to that of the third stage, which is described below.

This stage also is of short duration, probably about three days, or a little longer. There is little variation in size, for there seems to be little growth during this instar, most of the energies of the organism being occupied in building up the various organs of a typical dipterous larva—tracheal, circulatory, nervous, and excretory systems, as well as mouth-parts and muscles.

The measurements of this stage are as follows (12 specimens):—

	Smallest.	Average.	Largest.
Body length	·52 mm.	·54 mm.	·6 mm.
Tail length	·28 „	·45 „	·49 „
Total length	—	·82–1·05 mm.	—
Mouth-parts: –			
Pharyngeal sclerite, length	—	·087 mm. (·066–·117).	—
Mandibular „ „	—	·027 „	—
Dentate „ „	—	·024 „	—
Filaments on posterior abdominal segments:—			
Average length about ·015 mm.			

The Third Stage Larva.

The External Features.

The body of the third instar larva (Pl. I. fig. 3) is of the same general appearance as that of the stage just described, but the S-curve is more pronounced. The tails are actually and relatively very much longer. They are usually from 1½ times to twice the length of the body, but are variable; occasional specimens are found having them very much larger still. Apart from the broad basal part, they are of even diameter throughout, although now and again early third stage larvæ are found which are exceptions to this, having the tails as in the second instar. They are very fragile, and it is a difficult matter to dissect them out without injury. The mouth-parts are larger and somewhat different in shape, as the measurements given below will show, and provide a satisfactory means of distinguishing the different stages. The abdominal filaments are longer and are present on segments 5–10, with in some cases a few situated on the ventral side of segment 4.

This stage is of much longer duration than the two previous ones, amounting in all probability to ten or twelve days. A considerable amount of growth takes place as is indicated by the great variation in the size of the body, the mouth-part sclerites being, of course, constant in measurement and showing very little variation.

The larva is capable of a little more movement than its predecessor, although of the same type, transverse segmental muscles still being absent.

Third Stage Larva:—*Measurements* (*material unlimited*).

	Smallest.	Average (12 larvæ).	Largest.
Body length	·69 mm.	1·30 mm.	2·25 mm.
Tail length	·65 „	1·42 „ (circa)	4·35 „
Total length	1·4 „	2·72 „ (circa)	6·60 „
Mouth-parts:—			
Pharyngeal sclerite	·156 „	·169 „	·182 „
Mandibular „	—	·043 „	—
Dentate „	—	·043 „	—
Filaments on posterior segments:—			
Average length about ·11–·12 mm.			

The Sense Organs.

On the dorsal surface of the head is a pair of large sense organs (Pl. II. fig. 1), the *antennæ* (·022 mm. in length), consisting of a single segment, bearing three setæ at the apex. The *maxillary palps* are situated between the antennæ and the labral fringe.

Each palp is two-segmented, and bears at its apex two sensory tubercles, one about twice as large as the other.

The upper and lower "lips" are fringed with long filaments which move in unison with the manibular and dentate sclerite respectively.

A pair of single segmented labial palps, broad at the base and tapering to the apex, are situated ventrally immediately behind the mouth, often obscured by the mouth-fringes. They bear a few large setæ at the apex, with lesser ones visible on the sides.

A pair of conspicuous sense organs is situated on the dorsal surface of the 1st segment. These organs consist of simple tubercles ·009 mm. in length, with one or two conspicuous setæ at their base. They apparently correspond to the accessory sense organ described by De Meijere.

On the ventral surface of this same segment, situated far forward, immediately behind the labial palps, a pair of simple tubercles can be seen.

These apparently correspond to "Keilin's organ," and similar structures are found on the ventral surface of segments 2 and 3 about mid-way between the intersegmental furrows. They differ from those on segment 1 by their smaller size (·0065 mm.). In the majority of cases in which these organs have hitherto been described they consist of groups of four long hairs, in some cases raised on a tubercle, but more often on a level with the body-surface, so that the type found in *Cryptochætum* is unusual.

The Bucco-pharyngeal Apparatus and its Muscles. (Pl. II. fig. 1.)

The mouth-parts differ only in minor details from those of the previous instar. The mandibular and dentate sclerites are larger and more sharply pointed, and the pharyngeal sclerite is very much longer.

The trough which forms the greater part of the pharyngeal sclerite is, of course, the heavily sclerotised and pigmented ventral wall of the œsophagus. Anteriorly it is sclerotised for a very short distance dorsally, as well as ventrally, in the region of the hypostomal sclerite, but further back the dorsal wall is pliable, and can be expanded by the action of the pharyngeal dilator muscles which are attached above to the over-arching plate-like arms of the pharyngeal sclerite, the whole apparatus thus acting as a suction pump.

Posteriorly the *pharyngeal sclerite* dilates to form two lateral wings which serve for the attachment of the muscles working the *mandibular* and *dentate* sclerites.

As before, the *mandibular sclerites* are capable of independent movement, while the *dentate sclerites** ("are median ventral" of Keilin) are fused together in the median ventral line. The latter bear a row of minute teeth on the anterior edge, and thus form a heavily sclerotised serrate lower lip. The cuticle round the mouth is split into long filaments which form fringed upper and lower lips attached to the main hooks of the mandibular and dentate sclerites respectively; they thus move with the mouth-hooks, and seem to have the effect of drawing in a current of the liquid medium upon which the larva subsists.

In the median line, projecting from the floor of the mouth, is a tongue-like structure fringed in the same way and lacking sclerotisation, but capable of independent movement. If the living larva be watched under a high power of the microscope it is seen to be alternately protruded and retracted, apparently thus

* Doubtfully homologous with the dentate sclerite of Hewitt.

acting, in conjunction with the fringed mouth-parts and the pharyngeal dilator muscles, in producing an inward flow of food.

The *hypostomal sclerite* of Hewitt ("pièce intermédiare" of Keilin) is not present as a separate structure, but is fused on to the front of the pharyngeal sclerite, its position being indicated by the point of entry of the common duct of the salivary glands.

The *hypopharyngeal plate* (of Pantel, Thompson, etc.) is very small, and lies in the median line between the front end of the pharyngeal and the dentate.

The epipharyngeal plates (of Pantel) have not been observed in this stage, although they are easily seen in the final instar, and will be described thereunder.

I have purposely refrained from using the terms "mentum" and "cardo," used by De Meijere in his description of the larva of *Drosophila funebris*, as there seems no justification whatever for supposing the plates of the pharyngeal skeleton to be homologous with structures found in adult Diptera or in other insects.

The floor of the pharynx is devoid of grooves, and is typical of a carnivorous as opposed to a saprophagous larva.

The bucco-pharyngeal apparatus is provided with a complex set of muscles. The whole complex can be thrust forward by means of two pairs of muscles, the *dorsal* and *lateral cephalic protractors*. The first pair is attached on either side of the mid-dorsal line of the first segment, and runs to the posterior dorsal edges of the dorsal wing-plates. A separate pharyngeal depressor has not been observed. The *lateral cephalic protractors* ("ventral cephalic protractor" of Hewitt) run obliquely from the lateral margins of the dorsal wing-plates to the ventral part of the anterior margin of the first segment. The mandibular sclerites are worked by two pairs of muscles, the *mandibular extensors* and *flexors*, which are attached respectively to the dorso-lateral ridge and to the ventro-lateral part of the lateral plates. Both are broad at the base and narrow to a tendon-like insertion, those of the former pair passing over the lateral edges of the front end of the pharyngeal sclerite. Two similar pairs of muscles, probably equivalent to the "labial retractors" of Thompson, operate the dentate sclerite. They are inserted on the ventral part of the lateral plates, and probably correspond in part to the incorrectly-named "stomal dilator" and "mandibular depressor" groups of Hewitt. In addition, there is a muscle which runs from the mid-dorsal region of the body-wall, near the attachment of the *dorsal cephalic protractors*, the exact insertion of which has not been made out, but in all probability it corresponds to the "labial elevator" of Thompson, and is inserted on the dorsal wall of the pharynx. Finally, there is a pair of delicate muscles inserted far back on the mid-ventral portion of the pharyngeal sclerite, the anterior end of which appears to attach to the floor of the buccal chamber, and which is probably concerned with the movements of the median tongue-like structure described above.

A set of *internal pharyngeal* muscles are attached dorsally to the over-arching inner sides of the dorsal wing-places and ventrally to the dorsal wall of the pharynx. The whole "head" of the larva can be withdrawn by means of the *cephalic retractors*, which consist of six or seven pairs of muscles attached to the posterior margin of the "head," and comprising the ventral longitudinal and oblique muscles of the first two post-cephalic segments.

The Abdomen.

The External Features.

The numerous filaments present on the last six body segments deserve special mention. They are chitinous structures, annular at the base, with a narrow central cavity extending not more than one-third of the way up. All the rest is solid chitin, which stains strongly in hæmatoxylin and in Mann's Methyl blue-Eosin formula. There do not seem to be any special hypodermal cells associated with

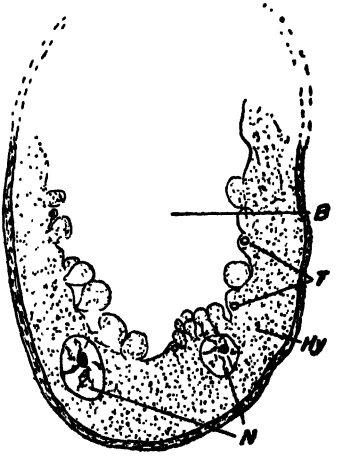
these filaments, and there is no suggestion of their being sensory. Their mode of attachment is shown in text-fig. 18.

It is difficult to suggest any possible function for them. At first sight it might seem that they were of value in increasing the area of surface of the larva, thus allowing of more efficient cutaneous respiration; but since they are chiefly solid chitin, it is difficult to see how they can be of much use in this respect.

The tails, which terminate the body, consist, as in the previous instars, of lobes of the body-wall covered with a chitinous cuticle of about 5 μ in thickness. Typically in the third instar they are strongly dilated at the base, where their width is equal to that of the last abdominal segment, but throughout the remainder of their length they consist of a long narrow tube about ·03–·04 mm. in diameter, with a blood-space reaching to the extremity.

The hypodermis of the tails consists of a single layer of cells with relatively enormous nuclei (diameter 22–32 μ). At the base the cell-walls are easily seen both in sections and in entire mounts, but nearer the tip, in the tubular

Text-figure 9.



Transverse section of tail of third instar larva, stained methylene blue-eosin, showing a secretory phase (oil imm.).

B. Blood space. *Hy.* Hypodermis. *I.* Tracheæ. *N.* Nuclei.

regions of the structure, I have been unable to distinguish them—the tissue having the appearance of a syncytium—and in this region the nuclei are considerably smaller. The nuclei are in many cases highly vacuolated. They project into the cavity of the organ as shown in (Pl. IV. fig. 1).

In one or two instances, sections (text-fig. 9) show a "secretory phase," globules of material, staining in a way very similar to the cytoplasm itself, projecting from the inner surface of the hypodermis into the lumen of the tail. The possible significance of this is discussed elsewhere in this paper.

There are no muscles, so the tails are incapable of independent movement; they merely float at random among the organs of the host.

The cavity is filled with blood, but as there are no pulsatile organs connected with the structure, there is no blood-movement other than a slight ebb and flow due to the movements of the body of the larva.

As mentioned in connection with the last instar, each tracheal trunk sends a

number of fine branches into the dilated base of the tail. Not infrequently the early third stage larvæ have the tails of the second stage type, in which case the tracheæ are seen looped and coiled in the basal region (text-fig. 8), but normally with the opening of the lumen of the tail throughout its entire length the tracheæ are carried down with the inflowing blood, extending, as a rule, for about two-thirds the length of the organ. They do not branch, and end blindly. The usual number is six in each tail, although eight, and in one case ten, have been observed. They have a diameter of about 3 μ, and are of the moniliform type described in certain tachinid larvæ (Thompson, 1928). When filled with air they have the appearance of a string of beads, and the same structure can easily be seen in sections (Pl. IV. fig. 2).

The Tracheal System.

The tracheal system of the third stage larva (Pl. I. fig. 4) consists of two main tracheal trunks running the length of the body and giving off a number (usually six) of fine branches into each tail, as already described.

There is a dense subcuticular network of fine tracheal branches originating from the main trunks in each segment. A well-developed transverse commissure is present in the last segment, and two rather slight ones in the fore part of the body. There are no spiracles.

The Fourth Stage Larva.

The External Features.

The fourth stage larva (Pl. I. fig. 5) is very different from any of the previous stages both in appearance and in mode of life. It is an ovoid yellowish-white maggot, tapering shortly towards the anterior end. There are ten clearly-marked segments behind the head, nos. 5 and 6 having the greatest diameter, each bearing a belt of minute spines on the anterior margin, the "warzengürtel" (De Meijere) or "ambulatory setæ." The belts on the first two post-cephalic segments are narrower than the rest.

The tails are an even more striking feature than in the previous instars, since they may be as much as 9·3 mm. long. Except at the bases, they are of narrower bore, and are kinked and irregular. They are brittle and are very easily broken in dissection. The gigantic nuclei, spaced out along the tail in irregular fashion, are conspicuous even under a hand-lens, since their position is often marked by a kink or swelling.

The larva is now amphipneustic, the spiracles being represented by a pair of heavily sclerotised dart-like structures sunk into pits on the front margin of the first segment, and a pair of powerful blackish-brown hooks at the hind end of the body.

The muscular system is completely developed, and with the completion of the transverse segmental muscles, hitherto lacking, the larva is capable of as much movement as most free-living dipterous larvæ.

Fourth Stage Larva.—Measurements (material unlimited).

	Smallest.	Average (12 larvæ).	Largest.
Body length	1·8 mm.	2·8 mm.	3·17 mm.
Tail length (very variable) .	—	6·3 „	9·3 „
Total length	—	Approximately 11 mm.	—
Mouth-parts :—			
Pharyngeal sclerite	·26 mm.	—	·32 mm.

The Mouth-parts.

The cephalic-pharyngeal skeleton (Pl. III.) is now more complicated than in the previous instar, and in general appearance is more typical of a free-living form. The pharyngeal sclerite is relatively shorter, and the whole apparatus is of stouter construction, although of the same general type. The general structure can be understood from the diagrams, and only the chief differences will be noted here.

The *mandibles* are much stouter and work diagonally, their points being directed inwards and downwards. Between them is seen an isolated boomerang-shaped sclerite (Pl. III. fig. 1, *Med.Dor.Scl.*) situated in the roof of the pharynx.

Below the mandibles, and projecting far forward in front of them, is the U-shaped *dentate sclerite*, similar to that of the last instar except that the teeth are more strongly developed; the median ventral part is more heavily sclerotised, and the lateral plate-like expansions each bears a circular semi-transparent area.

The *hypopharyngeal sclerite* is a small, slightly sclerotised plate situated on the floor of the pharynx overlapping the orifice of the salivary duct. It is roughly triangular in shape, and bears two pale circular areas near its front margin. On the roof of the pharynx, slightly in front of this, is seen the *epipharyngeal sclerite*. It is a small plate similar to the hypopharyngeal in appearance, but smaller and, like it, bears two pale spots which are apparently the terminations of the *epipharyngeal nerve*. The dorsal cross-piece, presumably part of the lost *hypostomal sclerite*, is very heavily sclerotised, and is conspicuous from above.

The sense organs of the head and first post-cephalic segment are closely similar to those of the third instar and do not require a separate description. Segments 2 and 3 appear to lack the sensory organs present in the second and third stages, although the numerous cuticular spines make it very difficult to be certain of their absence.

The *tracheal system* consists of two main longitudinal trunks terminated by conspicuous and heavily sclerotised spiracles. As in the previous instar, there is a well-developed posterior commissure in the 10th segment and less clearly defined ones anteriorly. Numerous fine branches are given off in each segment to form the subcuticular network, while those of the 10th segment, which originate from the main trunks close to the point of junction with the posterior commissure, supply each of the "tails" as before.

The Spiracles.

The anterior spiracles (Pl. II. fig. 2), seen under low magnification, appear to be simple, sharply-pointed, dart-like structures. They are situated each in a deep pit which opens on the fore margin of the first post-cephalic segment.

Under high magnification each spear-like spiracle is seen to consist of a number of minute buds, the great majority of which are closely adpressed to the main axis. A few, however, are turned back and project more or less at right angles from the shaft.

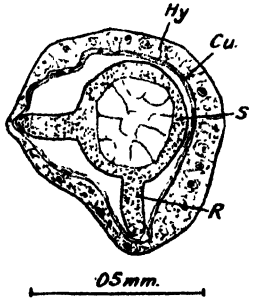
The whole structure is so heavily sclerotised and pigmented that it appears, on superficial examination, to be completely closed. It is almost certainly non-functional as a respiratory organ during the greater part of the larval life, since it is kept retracted within the spiracular pocket—indeed it seems doubtful if the larva has the power of extruding it until nearly ready for pupation. Closer examination, however, shows that each bud is hollow, with a very minute clear spot at the tip, and sections which pass through the reflexed buds reveal a very minute aperture. The felt chamber is divided up by numerous thin chitinous partitions, giving the whole the appearance of a tube filled with soap-bubbles (text-fig. 10). In section the spiracle often appears to be completely closed by these structures, but there are probably minute apertures which are not visible thus.

The tracheal trunk, just behind the spiracle, is thrown into a loop, as in

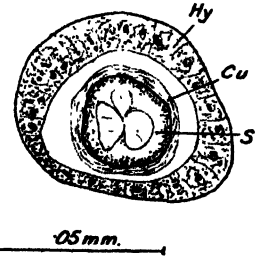
Drosophila and other dipterous larvæ, thus allowing the spiracle a very considerable amount of movement. Extrusion appears to be accomplished merely by pressure on the body-fluids exerted by the transverse and oblique muscles of the body-wall, but retraction is effected by the action of a pair of muscles of the first segment, which are attached to the hypodermis near the base of the spiracles.

The structure of the posterior spiracles is clearly seen from the diagram (Pl. II. fig. 3.) They are close together on the dorso-posterior surface of the 10th segment, and consist of a pair of powerful hook-like structures situated on a pair of heavily pigmented chitinous plates. Essentially the structure is very similar to that of the anterior ones; the felt-chamber is packed with the same chitinous spheres, and numerous buds are present, all of which, however, are closely adpressed.

Text-figure 10.



Text-figure 11.



Text-figure 12.

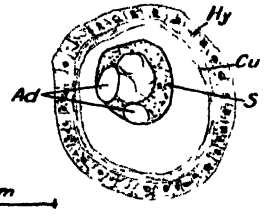


Fig. 10.—Anterior spiracle, fourth stage larva. Transverse section in region of two reflexed buds. *Cu.* Chitinous lining of same. *Hy.* Hypodermis of spiracular pit. *R.* A reflexed bud. *S.* Heavily chitinized wall of the spiracle.

Fig. 11.—Anterior spiracle, fourth stage larva. Transverse section through base. Lettering as text-fig. 10.

Fig. 12.—Anterior spiracle, fourth stage larva. Transverse section near tip. Lettering as text-fig. 10. *Ad.* An adpressed bud.

Instead of being sunk into a pocket, the spiracle is invested in a heavily pigmented chitinous sheath, an extention of the plates mentioned above, giving the whole hook a fossilised appearance. There seems little question that the posterior spiracles are completely closed. There are thin places in the spiracular wall near the apex of each bud, but I can find no suggestion of any actual openings. This is of particular interest since, according to Vayssière, the spiracular hooks of *C. grandicorne* each have an opening, and are inserted into one of the main tracheæ of the host (*G. serratulæ*), and a similar state of affairs has been recorded for *C. chalybeum* (De Meijère, 1916, p. 196). No such habit has ever been observed in *C. iceryæ*.

The Internal Anatomy.

The internal anatomy of *Cryptochætum* does not require very detailed treatment, for in spite of the peculiar mode of life and extraordinary external appearance of the larva, the intern... ...ne... ...cy... ...rhap... ...s
type. The description rete... ...erwis... ...ated

The Alimentary ...

The *fore gut* passes back from the mouth along the floor of the trough formed by the pharyngeal sclerite. Behind the pharyngeal apparatus the œsophagus narrows suddenly to a diameter of about ·02 mm., and continues thus for a short distance before passing between the *circum-œsophageal commissures*. Immediately behind it dilates to form a typical pyriform œsophageal valve, giving rise, in the last larval stage, to a strong peritrophic membrane not discernible previously.

The mesenteron is larger in diameter, and in structure varies considerably, according to the stage of development of the larva. In second and early third stage it runs almost straight, and diverticula are absent or very slightly developed. In the later third stage larvæ a pair of *gastric cæca* is developed near the anterior end of the mesenteron. Behind the region of the cæca the mesenteron is much larger, and forms an elongate sac till it narrows again at its junction with the proctodæum.

In the last larval stage the mid gut is much longer and is highly convoluted.

From the histological point of view the mid intestine does not require any very detailed description. The wall is composed of a single layer of epithelial cells of rather large size, and with the cell-walls somewhat indistinct. Externally there is a fine muscle layer.

In third stage larvæ the cells are for the most part flattened to form a pavement with a thickness of about 12–14 μ, the nuclei having a diameter of from 4–6 μ. The cytoplasm is homogeneous and the cell shows very little sign of secretory activity.

In the fourth stage larva the anterior region of the gut has a very similar structure. It is often greatly distended, and the cells consequently flattened and attenuated. In contrast to the third stage larva, the cytoplasm is often highly vacuolated. Further back much larger cells, having a diameter of 20–30 μ, are to be found, each cell bulging into the lumen of the intestine. The cytoplasm here is strongly vacuolated and shows signs of great activity. The nuclei have a diameter of about 8 μ.

The most striking difference between the third and fourth stage larvæ as regards the histology of the mid gut is in the great secretory and absorptive activity displayed by the cells in the latter case. It seems reasonable to assume that this is connected with the change from a diet consisting almost entirely of blood and pre-digested food to one of fat body and other tissues. It roughly coincides with a relative decrease in size of the salivary glands. Up to now the salivary fluid alone has been sufficient, but when the tissues themselves are devoured, digestive ferments of a different type are required.

The groups of small replacement cells described for so many dipterous larvæ and other insects have not been detected.

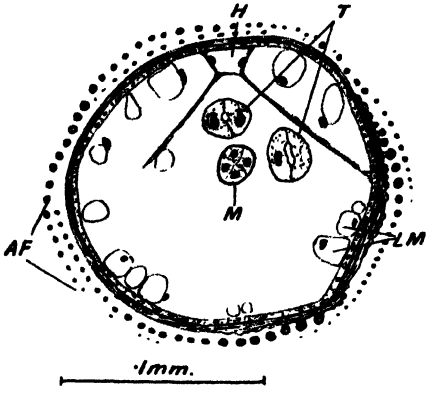
Posteriorly the mid gut narrows towards its point of junction with the hind gut in the 9th segment. The lumen becomes exceedingly small and is finally lost (text-fig. 13 and Pl. V. fig. 2), the mesenteron being completely closed posteriorly. It ends as a strand of cells attached to the wall of one of the malpighian tubes at the point where it enters the anterior end of the hind gut.

In the fourth instar the gut is open throughout its length, and defæcation is frequently observed.

The *hind gut* is widened anteriorly to receive the large malpighian tubes. It runs straight from the blind end of the mesenteron to the anus, which is situated between the tails. It is lined by a delicate chitinous membrane. The four

Malpighian ... the anterior end by a pair of ducts, the large terminal cells of which project far into the lumen, almost filling it.

Text-figure 13.



Transverse section of an early third stage larva at the region of closure of mid gut; showing also sections of the abdominal filaments and their mode of attachment.

A.F. Abdominal filaments. *H.* Heart. *L.M.* Developing longitudinal muscles. *M.* Mid gut. *T.* Malpighian tubules.

The wall of the hind gut is composed of from one to three layers of small cells with relatively rather large nuclei.

Circular muscles are very slightly developed in the third instar, but are conspicuous in the last larval stage. They are external to the basement membrane, and not intracellular as in *Calliphora* (Perez, 1910).

The Malpighian Tubules.

The *malpighian tubules* are four in number, and, as is usual with dipterous larvæ, are arranged in two pairs, each with a very short common duct. The longer pair runs forward to the region of the 7th segment, where each tube doubles back on itself for a short distance before ending blindly. The other pair is much shorter, and lies chiefly in the 9th segment. The tubes are of approximately even diameter throughout, and are very uniform in structure. Each in section is shown to be composed of a ring of two or three cells, which are about 12 μ in diameter, with large nuclei, in general appearance and staining reactions much like those of the salivary gland. The recurrent portion is not dilated and thin-walled as it is in *Drosophila* and many Muscids, and nothing in the nature of calcospherites could be observed.

The blind end of each anterior tubule is connected to the dorsal body-wall by a fine branch of one of the alary muscles of the heart (text-fig. 16). Similar muscle-connections have been observed by Pantel for *Ptychoptera* and by Eastham (1925) for *Drosophila*.

In the last larval stage the tubes are relatively very short, as little or no increase in length takes place.

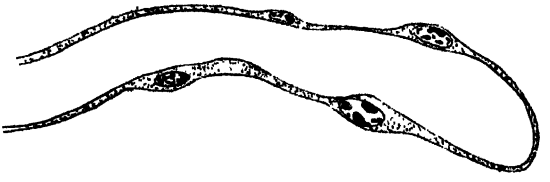
The Salivary Glands.

A pair of simple tubular *salivary glands* is present extending from the region of the œsophageal commissure as far back as the end of the ventral nerve mass. From each gland a duct of about 4 μ in diameter runs forward to join its fellow

beneath the pharyngeal sclerite. The common duct is very short, and almost immediately empties itself into the floor of the pharynx immediately behind the *hypopharyngeal plate*.

The anterior part of each gland is tubular and fairly narrow, having a lumen of about 26 μ in diameter. The wall of the gland is thick, and shows in transverse

Text-figure 14.

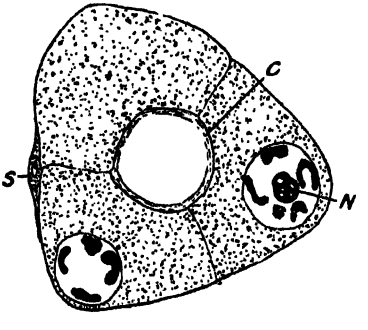


1 mm.

Longitudinal section through the terminal portion of salivary gland of early third stage larva

section as a ring of three to five or more large cells, about 12 μ across, with large nuclei (9 μ). Further back the gland usually dilates to form a large thin-walled sac (text-fig. 14) distended with a fluid which stains a bright pink with eosin. Different individuals seem to vary a good deal in the degree of distension and the consequent thickness of the wall, but the sac may be as much as 50 μ in diameter,

Text-figure 15.



1 mm.

Transverse section of salivary gland of last stage larva, stained methyl blue-eosin.
C. Chitinous lining to gland. *N*. Highly vacuolated nucleo us. *S*. Nucleus of sheath.

when it forms a most striking object in sections. The thin walls of the sac (2–3 μ or less) are composed of the cytoplasm of the cells, the large nuclei being seen as excrescences on the exterior of the gland. This dilation is more marked in the second and early third stages than in the late third stage.

In the last larval stage the gland is relatively smaller, being tubular and thick-walled throughout, with the lumen often quite small.

The large size of the gland in the earlier stages, as mentioned above, is probably connected with the quiescent state of the mid-gut epithelium at this time.

Sections of the gland of the last stage larva (text-fig. 15) fail to show any intracellular ducts such as are described by Frew (1923) in *Forcipomyia*. The gland is lined by a chitinous layer, and in occasional sections the nuclei of the sheath described by Keilin (1917) are to be seen. In many sections, however, this sheath cannot be distinguished, and it does not seem to envelop the whole gland. It is not fibrous as it is in the carnivorous Anthomyids and the Syrphids.

The nuclei of the glandular epithelium are very large and the chromatin bands are convoluted. The nucleolus is relatively enormous, and in some instances is highly vacuolated.

The Œnocytes.

The œnocytes (Pl. IV. fig. 4) are found as paired groups of tightly-packed spherical or somewhat pyriform cells arranged segmentally. Each group comprises some 15 to 30 cells lying in close association with the hypodermis about midway along the lateral margin of each segment from IV. to X. The cells vary from 30–35 μ in diameter, with a nucleus of about 12 μ across. These are mono-nucleate, with a large amount of cytoplasm which is slightly vacuolated, and the cell-walls are very distinct. Nothing in the nature of the projecting bubble-like vacuoles described by Kreuscher (1922) in *Dytiscus* and by Eastham in *Phœnoserphus* (1928) could be observed. Each group of cells is seen to be closely associated with one or two fine tracheæ of the moniliform type, from which numerous tracheoles penetrate the cells themselves Nothing corresponding to the radiating secretory canals described by Kreuscher could be seen.

The fat body is little in evidence before the final instar. In the second and third stages it is represented by a few loose strands of tissue chiefly noticeable in the region of the pharyngeal mass, and contains little or nothing in the way of fat or other stored-food material. Sections of larvæ at this time often appear almost "empty," owing to the almost complete absence of fat body and the slight development of the muscular system.

During the last larval stage, when great quantities of the fat body and other tissues of the host are devoured, much fat is stored, and a copious diffuse fat body, enveloping the gut and occupying the greater part of the hæmocœle, is developed.

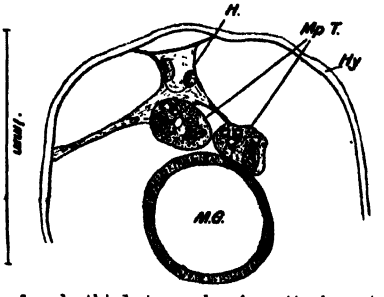
The Circulatory System.

The circulatory system differs little from the type which has often been described for Dipterous larvæ. The heart proper is closed posteriorly in the anterior part of segment 10, and extends to segment 8. In this region it is wide, and is bordered by very large pericardial cells (Pl. V. fig. 1), and is relatively larger in the last stage larva than in the previous instars. The nuclei of the wall also are large, and project far into the cavity of the heart. The alary muscles send fine attachments both to the dorsal wall of the proctodœum and, as has already been mentioned, to the malpighian tubules. They are easily observed in the third instar (text-fig. 16), particularly the early third, but I have not been able to detect them in the fourth, although they may exist. The intermediate region, as usual, is much smaller in diameter, and is bordered on either side by a string of very small pericardial cells. Beyond the level of the œsophageal valve the vessel slopes downward and, passing through a group of small cells which constitute Weismann's ring, lies in the groove between the supraœsophageal ganglia. Beyond this point I am unable to trace it.

The circulatory system appears, from sections, to be completely developed by the end of the second larval stage, but I have never been able to observe it in action before the beginning of the final instar.

This is all the more curious in consideration of the large number of experiments that were carried out on living larvæ, when the heart-beat should have been easily observed, for in the fourth stage, although the cuticle is thicker and more opaque, and the fat body more extensive, the heart-beat can easily be seen, the contraction of the dorsal vessel being visible as far forward as the 3rd post cephalic segment.

Text-figure 16.



Transverse section of early third stage, showing attachment of alary muscles to malpighian tubules.

H. Heart. *Hy.* Hypodermis. *Mp.T.* Malpighian tubules. *M.G.* Mid gut.

Indeed, until sections were cut it was supposed that the heart remained undeveloped till the last instar. It may be that, although fully developed, it does not become functional before, the slight contractions of the muscles of the body-wall and the movements of the gut keeping the fluids sufficiently in motion.

The Nervous System.

The *nervous system* consists of a small supra-œsophageal ganglion, the two lobes of which are divided by a deep median furrow and a large ventral nerve-mass or sub-œsophageal ganglion, connected by broad lateral commissures, just in front of the œsophageal valve. The ventral nerve mass extends back as far as the posterior margin of the 5th segment. The lobes of the supra-œsophageal ganglion project backward slightly above and on either side of the œsophageal valve.

Habits of Larvæ.

The first stage larva, being incapable of movement, floats in the body-fluids of the scale, and, since the eggs are laid more or less at random, may be found in almost any part of the host's hæmocœle. The food consists solely of substances absorbed directly through the very delicate cuticle.

Although, owing to the short duration of this stage larva and to the difficulty of finding it, sections through the fore gut were not obtained, yet the fact that it is closed seems established beyond doubt for the following reasons:—(*a*) Examination of whole larvæ, stained and unstained, under high power, failed to reveal any trace of opening, only a raised "scar" being present. (*b*) Mouth-parts are lacking. (*c*) The gut never contains any food material; when blood is taken in by the second stage larva it is easily visible owing to its colour. (*d*) When living larvæ were placed in normal salt solution and watched under high power no movement of the fluid in the vicinity of the "head" could be observed, although the peristaltic movements of the mesenteron were going on vigorously the whole time.

Since one of the main functions of the blood of insects is that of transport of the products of digestion to the various organs, it is doubtful whether the parasite at this stage has any need of digestive enzymes. As long as the larva is minute and

the proportion of surface to volume is high, the tissues of the larva can probably absorb all the food materials required, direct from their host's blood. In the *Cryptochaetum* larva, too, the method is probably rendered all the more efficient by reason of the large additional surface area presented by the two posterior lobes.

The reason for the peristaltic gut movement described above is obscure. The most likely explanation appears to be that the gut movements are of value in keeping the fluids of the larva in motion, thus serving, in a very rough-and-ready way, the function of the missing heart—an arrangement which suffices in many small Crustacea (Ostracoda, Copepoda) in which the heart is lacking.

The duration of this stage, though not exactly known, probably does not exceed two days.

In the second stage the mode of life is very similar, save that the food is absorbed by the mouth, which is now open, and which is equipped with well-developed mouth-parts. Owing to the orange-red colour of the blood of the *Icerya*, it is quite easy to see when the larva begins to take in food through the mouth, as the yellow fluid is clearly visible in the mid gut. The motion of the mouth-hooks and their fringed lips, together with the sucking action of the pharynx, the mode of action of which is described in detail in connection with the next larval stage, serves to draw in the food-material.

The food during this stage consists of blood with, perhaps, a certain amount of fat body digested externally, although the gut never contains any solid food.

The larva is still practically incapable of body movements, although it can, no doubt, shift its position slightly by means of the mouth-hooks. The duration of this stage is probably not more than three days.

The third stage is of much longer duration, in all probability three or four times that of the first and second.

Since the longitudinal muscles of the body-segments are now well developed, there is more movement, the oral segments being alternately withdrawn and protruded. The body movements consist of an alternative straightening and curving, increasing and decreasing the normal S-shape. Owing to the absence of transverse muscles, peristaltic movements of the body are not yet possible. The food during this stage is much the same as in the previous instar, although fat body is now destroyed to a greater degree. Occasionally some of the giant cells (up to 320 μ) of the salivary glands are ruptured, and sometimes other tissues are injured. This is not a regular feeding habit, and if the substance of the tissues is utilized it must be by external digestion, since sections fail to show any solid matter in the gut and chromatinic material is entirely lacking, although this becomes very conspicuous in the final instar.

Since the structure of the tails, with their large tracheal supply, suggested tracheal gills, it might be expected that these organs would lie in close proximity to the main tracheal trunks of the host or in any part where they would be likely to receive a particularly large oxygen supply. Sections of parasitized scale, however, show that they lie looped and twisted at random in the body-cavity or penetrating the fat body, and dissections confirmed this conclusion. Text-fig. 17 represents a half-grown scale cleared in cedar-wood oil, showing the mouth-parts of seven third stage parasite larvæ situated in various parts of the host and lying in different positions.

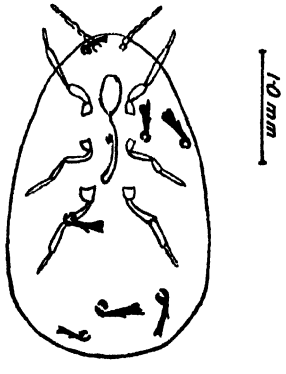
When the parasite enters on its fourth instar there is a considerable change in food habits correlated with the change in structure of the mouth-parts. The host is now becoming moribund and the contents of the body less fluid. The mandibles of the parasite work diagonally, and the dentate sclerite now has the serrate edge much more strongly developed. This apparently acts as a rasping structure, the tissue that is being devoured being pressed against it by the action of the mandibles. A great quantity of food is devoured in this stage, the much-coiled gut being filled with the bright yellow tissues of the scale.

Fat body, muscles, gonads, etc., are devoured, the alimentary canal as a rule being left intact till nearly the end, although if the host be a younger scale or overcrowded with parasites this does not always hold good. Just as the third stage larvæ, if crowded, may injure and kill each other, so now and again one finds cases in which the host's gut has been ruptured, but this is clearly abnormal. Defæcation now takes place freely. The tough peritrophic membrane surrounding the fæces is conspicuous.

Now that a well-developed muscular system is present, the larvæ can move easily. The peristaltic contractions of segments enable it to shift its position as necessities of food require, and the powerful hook-like posterior spiracles inserted into various organs doubtless give a strong purchase for the tearing action of the mouth-parts. It seems probable, too, that the lengthy tails, which are often inextricably entwined among the internal organs of the scale, also assist in this way.

As has been mentioned above, one case was found in which an egg was laid not in the body-cavity, but in the mid gut. This had hatched and developed as far as an early third stage larva when it succumbed, perhaps from lack of solid

Text-figure 17.



Parasitized scale cleared in cedar-wood oil, showing mouth-parts of seven third stage larvæ in various positions.

food. Presumably the liquid semi-digested sap in the gut was as suitable a food as the body-fluids of the scale, and only when it should normally have taken to devouring fat body was it unable to subsist. It is remarkable that the development could go so far without being affected by the digestive enzymes of the host.

As well-developed salivary glands are present from the second stage on, it seemed possible that external digestion might be taking place. However, a comparison of sections of parasitized and healthy scale at the same stage of growth revealed no observable difference in the general histology of any organ. There was no trace of any phagocytic reaction, nor, of course, is there anything corresponding to the inflammatory sheath produced by various insects as a response to injury of the hypodermis by Tachinid larvæ.

Occasionally the giant cells of the salivary gland may be destroyed, the larva occupying the space thus made available, but this does not seem to be a constant result of parasitism, and has only been observed in one or two cases. As has already been mentioned, it is by no means unusual for one female fly to lay several eggs in a single host, this being especially true when the rearing cages become at all crowded. The number of larvæ which mature depends, of course, on the size of

the host, but larvæ of the same age do not seem to have any injurious effects upon each other, at any rate while in the first and second stages, unless they are so numerous that there is an actual insufficiency of food. When, however, the third stage is reached, and especially when active destruction of the host-tissues commences, there seems to be more antagonism, for on several occasions I came across batches of third stage larvæ with two or three individuals dead and apparently mutilated. It seems most likely that when they get too crowded they are liable to injure each other in feeding. The injured ones then die, and thus the overcrowding is relieved. It is evident that this only happens when there is insufficient food, that is, when the larvæ are packed too closely, for if the host is capable of supporting them a large number will reach maturity without strife. I found one dead scale showing the exit holes of fourteen adult flies, and Riley (1889) has recorded an instance of seventeen flies emerging from one host, the scale in this case being *Monophlebus crawfordi* and the parasite probably *C. monophlebi*.

When, however, larvæ of different ages occur together in the same scale, it seems quite certain that there is antagonism of some sort, for one very rarely finds living young larvæ in the same scale with older larvæ. Similar well authenticated cases are recorded in the parasitic Hymenoptera (Timberlake, 1910; Spencer, 1926). This is, of course, in part due to the tendency of ovipositing females to avoid scales already containing the more advanced larval stages, but it is not the whole explanation. If, as sometimes happens, eggs are laid when third stage larvæ are already present, they seldom survive beyond the second instar. It does not seem likely that this is a case of mechanical injury. It may be that the older larvæ secrete some substance which is toxic to the earlier instars; but the most likely and the simplest explanation would seem to be that the older larva has so modified the internal conditions by its feeding, and later by its defæcation, that life is no longer possible for the younger. By the time the latter reach the fourth stage the host may even be moribund.

Towards the end of the last instar, when feeding is almost complete and the larva is preparing to pupate, the anterior spiracles, which have hitherto been retracted, are frequently thrust partially out of their pits, as if feeling for the body-wall of the host. This movement is apparently accomplished by increased pressure on the fluids in the fore part of the body, caused by violent contractions of the muscles of the posterior segments.

The larva moves about in the host till it succeeds in finding a thin region of the body-wall through which it can thrust its spiracles. This is generally, though not invariably, on the lateral margin of the scale, the parasite at time of pupation lying transversely. The actual position varies according to the size of the scale and the number of parasites contained.

If, as occasionally happens, there is just a single parasite in a scale too small to accommodate more, the full grown larva may so nearly fill the skin of its host that it is only possible for it to pupate longitudinally. Also, if a scale contains a large number of parasites, there may not be room for all to lie transversely and project their spiracles through the pleural region of the host, and some will have to be content with a diagonal position, piercing the dorsal or ventral surface.

When a suitable position has been found, the spiracles are thrust out to their fullest extent, projecting right through the host-skin, and being easily visible externally. The fore part of the body is now distended with a clear fluid, and the transformation to form a puparium takes place.

The host, if not already dead, soon succumbs, and the skin shrinks and dries, usually adhering closely to the lid of the parasite puparium. For reasons which are discussed elsewhere in this paper, it seems that the anterior spiracles have little (if any) respiratory function. They do, however, play a very important rôle in the process of pupation in that they make a preliminary break in the host's skin, so that when the fly is ready to emerge the pressure on the lid from within

easily produces a split which enables the insect to escape. The successful emergence of the fly is thus seen to depend on the thrusting out of the spiracles through a thin portion of the body-wall, such as the pleural region, with the insect lying in such a position that, as the skin dries and shrinks, it will be stretched tightly over the anterior region of the puparium and adhere closely to it. If this is accomplished, then the raising of the puparial operculum, with its attached "spiracular horns," by means of the pressure from the ptilinum, automatically enlarges the split and ensures a means of escape from the host. As in some other Agromyzids and in Drosophilids, the operculum does not as a rule break away entirely, but remains attached, its posterior border acting as a hinge. It should be noted, however, that the operculum is dorsal in position, as in the latter group, and not ventral, as is described by Miall and Taylor (1907) for the Holly-fly (*Phytomyza*).

Such a method of pupation is unusual, although not unknown, among parasite Diptera. The majority of Tachinids leave their host in the last larval stage, but *Carcellia gnava*, parasitic on *Malacosoma neustria*, is an exception to this, and Thompson records that some individuals of *Masicera senilis* Meig. will pupate in the dead host, *Pyrausta nubilalis*, although external pupation is the rule. Among the Dexiids, *Fortisia fœda* Meig. pupates in the dead body of its host, *Lithobius*.

Since, however, many of the leaf-mining Agromyzidæ have learnt to pupate in the mines, and emerge in much the same way, in this case the dead cuticle of the leaf adhering to the puparium and dehiscing with it, it is not very surprising that *Cryptochætum* has been able to solve a similar problem.

The Puparium.

The external features of the puparium are well shown in text-fig. 18.

The colour, at first pale yellow, rapidly changes with the hardening process to a dark brown, and eventually, as the fly matures, almost to black. The spiracular processes are brownish black. Ten segments are clearly visible, the first three taking part in the formation of the operculum, which opens on the dorsal surface. The line of fracture thus consists of the usual horizontal line of dehiscence plus the ascending branch, as in Drosophilids, and not the descending one, as described for *Phytomyza* by Miall and Taylor, thus making the operculum dorsal, not ventral. It is, in fact, a misnomer to call many of these flies "cyclorraph," and, as Miall pointed out many years ago, the term is very ambiguous, and, moreover, it is uncertain whether it was originally intended to refer to the dehiscence of the larval or the pupal cuticle.

The old larval pharyngeal skeleton remains in the puparium, lying on the ventral surface just behind the spiracles. Along the side a row of eight slightly dark spots, suggestive of spiracles, can be distinguished. The belts of setæ of the last larval stage are still easily visible under a high power with suitable lighting.

The tails, which are now shrunken and brittle, remain attached, although very easily broken off in dissection. When they are removed a small scar is visible, marking the point of attachment on each side of the anal scar.

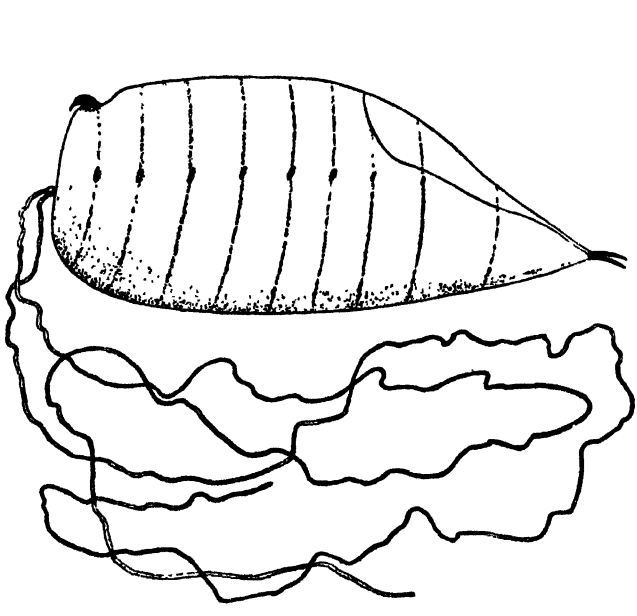
Contrary to what has been described (Keilin, 1921), in various phytophagous Agromyzids the stiffening of the puparium does not seem to be due to calcium carbonate. No effervescence was produced when in contact with hydrochloric acid, and prolonged soaking in acid produced no softening. This was also found to be the case when *Leucopis* puparia were tested in the same manner. This is correlated with the absence of calcospherites in both these forms, and in neither of the insects have I found calcium carbonate in the malpighian tubes.

The pupa within the puparium shows a pair of pupal spiracles on the anterior margin of the prothorax just in front of the base of the wing-sheaths, and almost

touching the eyes. They are purely internal, having no connection with any aperture in the puparial case.

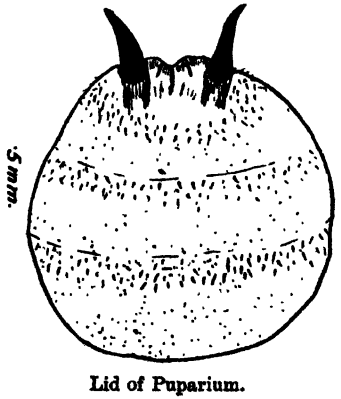
The pupal cuticle is very thin and envelops the animal loosely. I was quite

Text-figure 18.



Puparium.

Text-figure 19.



Lid of Puparium.

unable to distinguish any pre-pupal stage with a separate moult such as is described by Snodgrass (1924) in *Rhagoletis pomonella*. This is, of course, quite a different matter to what is usually called the pre-pupal stage, which is merely a period of quiescence without a separate ecdysis.

Discussion.

Since in none of the families of flies most closely related to *Cryptochætum* are any truly parasitic forms known, the study of the elaborate structural and biological adaptations of this insect to a parasitic mode of life is the study of a separate and restricted line of evolution of parasitic habits among insects.

The Primary Larva.

The first stage larva of *Cryptochætum* the "embryo larva"—as it may be called—is quite unlike anything that has hitherto been described in the order Diptera. Although the method of feeding by direct absorption through the cuticle is paralleled by the larvæ of Strepsiptera * and by the early stages of many Tachinidæ—*Thrixion*, for example—in no other case is there a complete absence of mouth and mouth-parts. In *Thrixion* the food is absorbed through the closed secondary sheath by a similar process which Pantel has called "physiological filtration," but the larva inside the sheath already has an open mouth and a complete buccal armature. (Fabre, it is true, described the first stage larva of the Bombyliid *Argyramœba* as lacking mouth-parts, but this, according to Lundbeck (1907), was due to his mistaking the posterior region of the larva for the head!)

There is, however, a very remarkable resemblance to the first stage larvæ of certain Hymenopterous egg-parasites. In the Chalcid *Polynema*, parasitic in the ova of *Agrion*, the egg hatches out as a flask-shaped sac of cells which, after five or six days, moults to form the extraordinary "*Histriobdella* larva" first described by Ganin (1869). Ayres (1884) has also described a similar stage between the hatching of the egg and the development of the "spindle-shaped larva" in *Teleas*. He describes it as a naked completed blastosphere which develops without a moult into the "spindle shaped" or "teleaform" larva which he reckons as the first true larval stage. He states that embryonic membranes are totally absent. The abortive "asexual larva" described by Silvestri (1906) in *Litomastix* also exhibits many points of resemblance to *Cryptochætum*, notably in the incomplete gut and the absence of heart.

It is generally supposed that the very simple types of larvæ which are so characteristic of the parasitic Hymenoptera have been produced by a tendency to emerge from the egg in progressively earlier embryonic condition. It is well known that the eggs of many of these forms contain very little yolk, and the individual is thus compelled to emerge in a more or less undifferentiated condition. In the case of parasites in which the larva, on hatching, is bathed in a nutrient medium, this early emergence has no ill effects, and since for a parasite to have a minute egg, *i. e.*, one lacking in yolk, is often a distinct advantage, we find that the process has been carried to extreme lengths. In some instances, such as those cited above, the embryo has no difficulty in continuing its development as a naked embryo in the blood of its host, whereas in others the chorion is capable of great distension, and the egg itself grows, the process of absorption of food material often being affected through the medium of a trophamnion.

Berlese (1913), as is well known, extended this idea, and supposed the varied types of insect larvæ to have been produced merely by eclosion of the embryo at different embryonic stages, so that in general the type of larva which emerged upon hatching depended upon whether the event took place at the protopod, polypod, or oligopod phases of development, or, in other words, upon the amount of yolk present. The theory obviously cannot be pushed too far, for there are many truly adaptive characters which arise *de novo* in insect larvæ, and cannot in any way be described as embryonic.

Again it is of the very essence of animal development that the organs should

* In the Strepsiptera, although an open mouth is present, food is apparently never taken into the gut, which is closed posteriorly (Nassonov, 1910).

develop at different relative rates in different forms. so that there are bound to be many cases in which, while one set of organs has attained a state of differentiation characteristic, say, of the oligopod stage, others will have lagged behind and will suggest the protopod or polypod stages.

Nevertheless there is no doubt that the theory, in a general way, throws much light on the subject of insect metamorphosis, and it is interesting to consider whether the first stage larva of *Cryptochætum* can legitimately be assigned to any one of the main types.

There seems little doubt that all the most striking characteristics of the primary larva can be described as embryonic. The absence of segmentation, mouth-parts, nervous system, sense organs, tracheal system, spiracles, salivary glands, muscles, and heart are all clearly due to premature eclosion, while the incomplete gut and the rudimentary malpighian tubules can easily be accounted for in the same way. In short, the only structural peculiarity which is not of this order is the pair of finger-like lobes at the hind end of the body. The complete absence of segmentation in the abdomen and the lack of sense organs and mouth-parts seem sufficient to show that this form corresponds to the true protopod stage of Berlese—far earlier than any other known Dipterous larva, and approximately equivalent to the later primary or early secondary stages of *Polynema* or to the intermediate form between the naked blastosphere and the primary "teleaform" type of *Teleas*.

As we should of course expect, the second stage larva shows a completed abdominal segmentation and a fully-developed buccal armature, with the usual sense organs on the "head" and thorax. Unfortunately in Diptera the most important criteria, namely, the abdominal appendages, are lacking, and even in many Hymenoptera these are so variable in development that they cannot be relied upon. However, the discovery of polypod larvæ by James (1928) in the Cynipidæ and by Eastham (1929) in the Proctotrypidæ gives very strong reasons for believing that such forms as the primary larvæ of *Teleas*, *Polynema*, and *Eucoila* are truly protopod.

In order to establish definitely the reason for the early eclosion of parasitic forms, it would be necessary to show that the eggs of these insects contained a smaller proportion of yolk than those of their free-living relatives which hatch at a later embryonic phase. This is no doubt true in Hymenoptera as a whole, although with the exception of a few outstanding cases, such as some of the Proctotrypid and Cynipid egg-parasites and the polyembryonic Chalcids, really satisfactory information on the subject is lacking, and would be very difficult to obtain. It is often assumed that the great increase in size of the eggs of many parasitic Hymenoptera is due to absorption of food-material, and is, therefore, indicative of lack of yolk, but there is, of course, no evidence to show that this effect may not be due solely to imbibition of water.

The egg of *Cryptochætum* is very minute and appears to be deficient in yolk, but beyond that little can be said. A comparison with the egg of the allied fly *Leucopis bella*, which, since the newly-hatched larva is an active free-living predator, should theoretically contain much more yolk, showed nothing of significance, the size of the egg relative to that of the mature larva being almost identical with *Cryptochætum*. The relative size of the egg, which is, of course, only the roughest guide to the amount of yolk present, is all the information that can be extracted from the average life-history paper, and is, perhaps, of some interest. A search through the literature as to the relation between dimensions of egg and of mature larva yielded information concerning some 30 or more species of Diptera belonging to 17 families. From this it is clear that, while the majority of free-living Diptera have a relatively much larger egg than *Cryptochætum*, there are one or two striking exceptions, e.g., *Chironomus*. The eggs of free-living Muscids and of many Nematocera are relatively much larger.

Among the parasites, some Tachinids have eggs which are relatively much smaller than *Cryptochætum*, although the larvæ on emergence are far beyond the protopod stage.

The later Larval Stages.

The later larval stages are sufficiently similar for them to be considered together. It is interesting to attempt to group their various structural characters according as to whether they are relics of a free life, and characteristic of the Agromyzidæ in general, or whether they are adaptations to a parasitic existence.

Structures characteristic of a Free Life.

1. The ambulatory setæ, or "Warzengürtel," which are found in the final instar, are quite typical of the the Agromyzidæ and allied groups, and their function in the free-living forms is obvious. It seems equally obvious that they can be of no value to *Cryptochætum*, and that they are merely a relic of the ancestral type.

2. The larval mouth-parts conform closely to the general Agromyzid type, which is characterized by a tendency to fusion and a resulting simplicity. The absence of a distinct *hypostomal* is an Agromyzid character * which is shared by the Conopidæ and some Ephydridæ. The same tendency is also exhibited to a lesser degree in the Oscinidæ (*Meromyza*, *Chlorops*), and in the Opomyzids (*Balioptera*), Frew (1923). On the other hand, the Drosophilidæ, Scatomyzidæ, Sapromyzidæ, Ortalidæ, Trypetidæ, and, as far as our knowledge goes, most of the remaining Acalyptrate families, approach the more complicated carnivorous Anthomyid pattern. The great development of the dentate sclerite, with its attached muscles, may perhaps be regarded as an adaptation to a carnivorous habit consequent upon a parasitic life. No such structure appears to be present in phytophagous Agromyzids, and it is also lacking in *Leucopis bella*. Although often well developed among carnivorous Anthomyids, it is unusual for it to exist in a truly parasitic form. The smooth ventral wall of the pharynx is well known to be characteristic of biontophagous as opposed to saprophagous larvæ.

3. The digitate spiracle, from which that of *Cryptochætum* has clearly been derived by a relatively slight modification, is very characteristic of the Agromyzidæ and allied groups.

Structures characteristic of a Parasitic Mode of Life.

(a) *Modifications of Pre-existing Structures.*

1. The slight development of muscles in the early larval stages is correlated with the lack of need for any means of locomotion, and is also very characteristic of many Tachinid larvæ. This is commented upon by Thompson (1928), who states that the larva of *Digonichæta* appears almost empty in section, as compared with the non-parasitic *Miltogramma*.

2. The retention of the apneustic condition till the last larval stage is, as far as I am aware, unique among the Agromyzidæ, although it is the rule for the first larval instar in this group to lack functional spiracles. The corresponding delay in the development of the tracheal system is also worthy of comment. The general build of the spiracles and their resemblance to allied free-living forms have already been dealt with. Their heavy sclerotisation to form piercing structures and attachment hooks is clearly a modification suited to an endoparasitic life.

3. The buccal filaments, while not unique structures, are more highly developed in *Cryptochætum* than in any other larva known to me, and may possibly be of special value to a form subsisting solely on liquid food.

4. The complete closure of the mesenteron in all but the final instar is a very rare condition among Diptera, although it is, of course, common enough in the Hymenoptera and throughout the Neuroptera Planipenna. In *Digonichatea* (Tachinidæ) the mesenteron narrows greatly at the point of junction with the hind

* According to Miall & Taylor, however (Tr. Ent. Soc. 1907), it is present in *Phytomyza aquifolii*.

gut, but no case of complete closure has, so far as I know, been recorded within the group. The only instances of complete closure previously recorded among the Diptera appear to be those in which viviparity takes place, and the whole nourishment of the larva is obtained from the uterine glands of the mother (*Glossina* and *Pupipara*).

The value of such a condition in parasitic forms appears to lie in the fact that poisoning of the host by toxic excretory products is avoided for as long a time as possible; moreover, a diet of blood leaves little fæcal residue, nor in the viviparous forms nourished on a special secretion would much waste matter be produced. A reason for closure in the Neuroptera is harder to find.

(b) *Production of New Structures.*

The only adaptations which can with any certainty be described as new structures are the tails and their contained tracheæ. The subcutaneous tracheal supply, too, is so highly developed that it might also be included here. The rings of abdominal filaments in the second and third stages have no counterpart in free-living forms, but their purpose is so problematical that perhaps they should not be included among adaptations.

Respiratory Function of the Tails.

One of the most striking facts about the biology of *C. iceryæ* is the absence of any connection between the tracheal system and the outside air during by far the greater part of the larval life. In this respect it is an exception to the general rule among the parasitic Diptera that, sooner or later in the larval life, connection with the atmospheric air or with the tracheal system of the host must be made.

The posterior spiracles, as we have seen, are closed, but the buds of the anterior pair are open, although even so it is a question whether they can be of any value. I have never observed them thrust out through the body-wall of the host until the larva is about to pupate, so that atmospheric air can be practically ruled out as a source of oxygen, nor have I ever seen them inserted into the tracheal trunks of the host.

There remains the possibility that they may from time to time rupture the finer tracheæ in the tissues of the host and absorb the gasses thus set free, but it seems very doubtful if the air absorbed in this way can amount to anything but a very small percentage of the total requirement.

The ingenious suggestion of Timberlake (1912), made with regard to *Limnerium*, that an appreciable part of the oxygen supply may be derived from the enormous quantity of tissues devoured, the contained oxygen being absorbed through the gut-wall, might also be applied to *Cryptochætum*. While impossible to prove, it seems quite feasible, and is worth bearing in mind.

Since the respiration throughout the greater part of the life must be cutaneous, the suggestion presents itself that the long caudal filaments are tracheal and blood-gills serving for the abstraction of dissolved oxygen from the blood of the host, in a manner somewhat similar to the action of the extraordinary external tracheal system of the third instar of *Comys infelix* (Embleton).

The circumstantial evidence for this view is very strong, and, in addition, there is a certain amount of experimental evidence. The very thin chitin of the walls and the abundant tracheal supply suggest tracheal gills. Anal blood-gills, similar in position, although not known in any near relatives of *Cryptochætum*, are of common occurrence in aquatic Dipterous larvæ.

Again, in Tachinids plates of epithelial cells which Pantel (1901) interprets as respiratory structures have been observed surrounding the anus. According to this writer, these pads are part of the proctodæum itself, and in the primary larvæ exist in the form of eversible sacs, capable of being thrust out at will. He regards

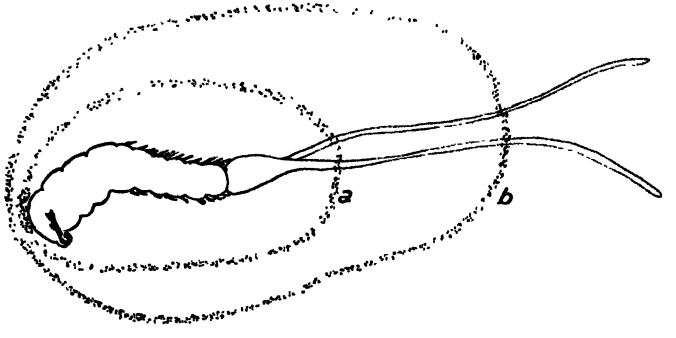
them as respiratory structures because their development is in inverse ratio to that of the tracheal system. He says:—

"Ces diverses circonstances semblent bien impliquer une fonction respiratoire. L'organe n'est pas une *branchie trachéenne*, car il a des parois épaisses et ne recoit pas un grand nombre de trachées, mais il peut être classé parmi les *branchies sanguines* de Miall et Hammond. Peut être serait-il mieux appelé *glande branchiale*, les caractères histologiques et physiologique de ses éléments donnant a penser qu'ils absorbent les liquides chargés d'oxygène comme ceux de l'épithélium intestinal les liquides chargés d'autres aliments.

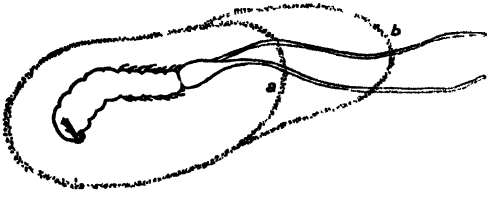
"Ajoutons pour terminer que la vesicule anale des Tachinides doit sans doute être homologuée à celle des Braconides et probablement aussi aux branchies sanguines des Nématocères."

Experiments on these and other endoparasitic larvæ, which will be fully

Text-figure 20.



Text-figure 21.

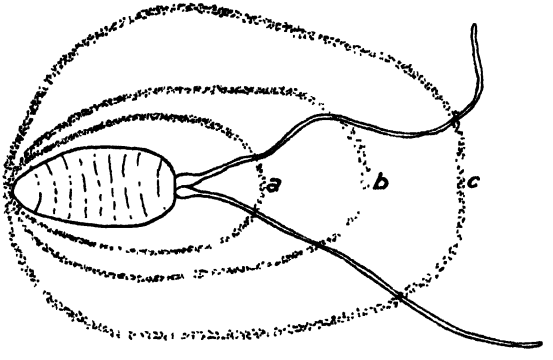


Types of flagellate band formation with third stage larva of *Cryptochætum*. The small letters indicate successive positions of the same band.

described in a separate paper, were undertaken in the hope of securing some evidence as to the function of these organs in *Cryptochætum*. They may be very briefly recounted here. The methods used were based on those employed by Fox (1920–21) for the study of the respiration of small aquatic organisms. The larvæ are dissected out of the host into normal salt solution. Carbon dioxide output can be studied by means of a suitable pH indicator, the larva being held motionless in a film of fluid under a raised coverslip, and the colour-change watched under a low power of the binocular microscope. The indicator used must have a colour-change in the region of pH 7·0 sufficiently intense to be easily visible, even in dilute solutions, in the thin layer under the coverslip. A large number of experiments carried out in this way with a variety of indicators gave the results which were expected on theoretical grounds, namely, that CO_2 elimination takes place freely over the whole body-surface, and is not confined to any particular organ or tissue.

The oxygen uptake is studied in a similar way, the indicator in this case being a culture of flagellates (*Chilomonas*, *Bodo*, etc.), or other motile Protista, which are positively chemotactic to concentrations of dissolved O_2 lower than that in the water saturated with oxygen at atmospheric partial pressure. The culture liquid

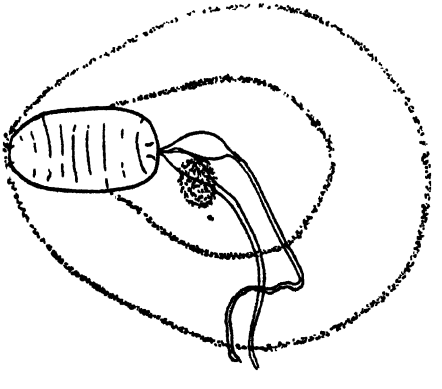
Text-figure 22.



Types of flagellate band formation, last larval stage.

is first strained through bolting silk and thoroughly aerated, and is run in under the coverslip. The flagellates, at first evenly spread throughout the fluid, are soon attracted to any region where oxygen is being abstracted from the medium, and consequently tend to form aggregations at points on the surface of the larva where

Text-figure 23.



Types of flagellate band formation, newly-formed puparium.

respiration is proceeding most actively. As the O_2 tension in the fluid falls below the optimum the organisms retire towards the edges of the coverslip (*i.e.*, towards regions of higher O_2 tension) in the form of an ever growing band. They thus retire first from the most actively respiring surfaces of the larva, and thus these regions form the foci for the band-formation. Text-figs. 20–22 show band-formation in

third and fourth stage *Cryptochætum*, the figures given being typical examples selected from a large number of experiments. It will be seen that these experiments suggest that, while respiration is undoubtedly going on over the whole surface, the region at the base of the tails is considerably more active than any other part of the body-surface, and accordingly it seems probable that this is the main function of these structures. If this is so, then their tendency to increase in length as the larva increases in size is explained up to a point.

There are, however, certain difficulties which the gill hypothesis, or, indeed, any other theory, leaves unexplained, the greatest of which is to account for the enormous length attained by the tails in the final stage. It is difficult to conceive how the terminal third or more of the structure can be of any use at all, for as there is no blood-flow in the cavity diffusion must account for everything.

If we reject the respiration hypothesis as being insufficient, there are three possible alternatives. Either (1) the tails are for the storage of excretory products; (2) they are concerned with the absorption of food-material by osmosis; or (3) they elaborate digestive secretion which acts upon the host-tissues externally.

In the first case no sign of excretory products can be observed in the tails, unless the chitin itself is the excretory product. While not impossible, this theory has little to support it, and it explains nothing. Convincing evidence for the third hypothesis is also lacking.

The second hypothesis would fit the facts well as regards the earlier stages. Before the mouth is open a large absorptive surface would be an asset, and even in the second and third stages a gut which has no through current is not a particularly efficient mechanism for dealing with a large bulk of liquid food.

The histological structure of the hypodermis, too, is very suggestive of an absorptive tissue. Miss A. Bidder has pointed out to me the curious resemblance between the tail hypodermis, with its huge highly vacuolated nuclei with very strongly-marked nuclear membrane, and the yolk-absorbing syncytial tissue which forms the vitelline membrane of the embryo of *Loligo vulgaris*. Trials with Sudan III. failed, however, to indicate that fat absorption was taking place, and I have not yet had opportunity to make more elaborate tests.

Although the majority of sections show no suggestion of absorptive or secretory activity, one set is, as has been mentioned above, an exception. In this case globules of material are seemingly being discharged from the epithelium into the lumen of the organ, the whole looking somewhat like a section of mid gut in active secretion. It seems possible, therefore, that a secondary function of the tails may be, under certain conditions, to supplement the alimentary canal in the absorption of dissolved food-stuffs, passing them from the blood of the host to that of the parasite. This hypothesis, however, fails to explain the great increase in size of the tails at the beginning of the last stage. The whole gut of the larva is then open and it is feeding ravenously, so that any other means of nutrition would seem to be superfluous. Moreover, since there is no mechanical means of transporting food-material within the lumen of the tails, it is difficult to imagine them as being at all efficient for this purpose.

These various possibilities have been dealt with at some length because of the bearing they have on certain isolated facts which are known concerning other species of the genus. No other species has been studied in detail, but De Meijere (1916) has given a very brief account of the last larval and the puparial stages of *C. chalybeum*, and Vayssière (1926) has described two later larval stages and has given some notes on the biology of *C. grandicorne*. Both these species have tails resembling those of *icerya*—in the former case equally highly developed, in the latter markedly less so. Neither author describes the tracheal system in detail, but both state expressly that they could find no trace of trachea in the caudal filaments, and both described the hook-like posterior spiracles as being open and

inserted into one of the main tracheal trunks of the host. As a result both are inclined to attribute to the tails the function of food-absorption after the manner of the "roots" of *Sacculina* or the second antennæ and mandibles of the extraordinary Copepod *Monstrilla*, parasitic on sedentary Polychæts. In the case of *grandicorne* there is the same objection to this theory as there is in *iceryæ*, for mouth-parts are well developed and apparently functional, and such a mode of feeding would seem quite unnecessary. In *chalybeum*, however, this may well be their function, for it seems not unlikely that a detailed study will reveal that the opening of the fore gut is even longer postponed than in *iceryæ*, since De Meijere (1916), speaking of the third stage, states that he was unable to observe the buccal apparatus. He says (p. 195): "Von Mundhaken habe ich nichts beobachtet, auch ist das ganze Schlundgerüst wenig entwickelt, von blasser Farbe."

It seems, therefore, more than probable that the tails serve quite different functions in the different species, and for which of these various purposes they can originally have been evolved is problematical.

The matter can only be settled by a thorough investigation into the life-history of these species, but it is certainly remarkable that members of the same genus, only with difficulty distinguishable as adults, should exhibit such great differences in the structure and biology of the larval stages.

Comparison with other Species.

Besides the points connected with the mode of respiration, there are other ways in which *iceryæ* appears to differ markedly from other members of the genus and, indeed, from all other closely-allied Diptera. The most striking of these is concerned with the number (and form) of the larval stages and their relation to the law of "le trimorphisme larvaire." Keilin (1915) drew attention to the fact that all the Cyclorrhapha in which the life-history has been followed have three larval stages separated by two moults. He also points out that the greatest morphological differences are, as a rule, between stages I. and II., so much so that it is almost more correct to speak of "le dimorphisme larvaire." The additional stage in *Cryptochætum* is quite clearly the first or "embryo larva" stage, and, as has been mentioned, is easily accounted for as a parasitic adaptation brought about by means of premature eclosion. The second point is rather striking, since in *C. iceryæ* there is a far greater difference in almost every character—alimentary canal, mouth-parts, tracheal system, and body form—between the third and fourth stages, which on the above hypothesis correspond to the second and third stages of other dipterous larvæ. The moult from second to third stage I have never actually observed, but the differences in all the measurements, as well as in the degree of development, of the tracheal system and tails and in the structure of the mouth-parts are such that it seems inconceivable that they are not distinct instars.

Still more curious are the apparent differences between *C. grandicorne* and *C. iceryæ*. Vayssière in his notes on the former species mentions three larval stages, but does not describe any "embryo larva" stage, his first stage resembling in a general way stages II. and III. of *iceryæ*. It hardly seems possible that the "embryo larva" could be present in one species and not in the other, and there seems no doubt that he has missed this form, which, owing to its transparency and minute size, it is very easy to do. Also he does not describe the egg, so would not be aware of the great discrepancy in size between it and his "first stage." I hope later to have the opportunity to investigate this species thoroughly, but, thanks to Professor Silvestri, I have already been able to procure female specimens for dissection, and have examined the egg, which measures ·29 × ·09 mm. The "first stage" as figured by Vayssière has a total length of at least 1 mm., which makes it seem all the more probable that an intervening stage is present.

Vayssière also alludes to a short-lived second stage with mouth-parts identical with the first, but having lost all trace of segmentation. The description is so slight that it is difficult to tell what this can represent. Nothing of the sort is to be found in *iceryæ*, nor is there any similar transient intermediate form between stages III. and IV., for larvæ undergoing this moult were observed on several occasions.

There the matter must rest till further information is available. It is idle, without a great deal more knowledge, to speculate upon the mode of evolution of parasitic habits in this group. That *Cryptochætum* was evolved from some form resembling *Leucopis* or *Chloropisca* in habit is more than likely, but the step from unspecialized predators of this sort to the elaborate parasitic adaptations here described is a big one, and we have no inkling as to how it was accomplished.

Summary.

1. The life-history of *C. iceryæ*, parasitic on *Icerya purchasi* in California, is here described. It represents a separate and restricted line of evolution of parasitic habits among insects.

2. The egg is laid in the hæmocœl of the host, usually during the second instar.

3. The primary larva is a minute "embryo-larva" of a type hitherto undescribed in Diptera, but known among parasitic Hymenoptera. It lacks tracheal system, heart, mouth, mouth-parts, and sense organs, and is without segmentation. It absorbs its food by osmosis direct from the blood of its host.

4. The second and third larval stages are tracheate but apneustic. They are remarkable for the lengthy tubular tails at the posterior end of the body, containing blood and tracheæ, and which increase in length with each instar. Mouth and mouth-parts, sense organs and heart are now normal, and segmentation is complete. The mid gut is still closed posteriorly in correlation with the plasmophagous mode of life. The muscular system is poorly developed, no circular muscles being present. There is a dense subcuticular network of tracheæ.

5. The fourth stage is omnivorous. The hind gut is open and the mouth-parts much modified. Anterior and posterior spiracles are now present, but the anterior ones only are open, and these are apparently non-functional till the time of pupation.

6. As many as 17 larvæ may come to maturity in a single host. The presence of late-stage larvæ appears to have an inhibiting effect on the development of the earlier stages.

7. A series of experiments with O_2 and pH indicators indicates that respiration is carried on at the general body-surface, but that the tails are especially important as tracheal gills for abstracting dissolved O_2 from the blood of the host. From a study of the histology of these organs it appears probable that in the earlier instars they also function as additional organs for the absorption of food-material by osmosis.

8. From what little is known of other members of the genus it seems clear that there are great differences both in structure and life-history between very closely related species.

9. The pathological effects upon the tissues of the host are very slight during the plasmophagous stages.

10. The puparium is formed in the dead body of the host. The stiffening of the puparial case is due to some substance other than $CaCO_3$. The mode of dehiscence resembles that of the Drosophilids rather than the Agromyzids.

11. The internal anatomy of the larva is described. It is chiefly remarkable for the closure of the mid gut posteriorly until the final instar.

12. The adult is short-lived and intolerant of captivity. Mating is described. About 200 eggs are laid. The female can apparently distinguish a scale containing advanced parasite larvæ from one unparasitised. A high proportion of eggs are infertile, in one case amounting to 20 per cent.

13. The adult is described, and diagnostic characters for distinguishing it from closely-allied species are given.

14. The structure of the antenna was investigated, and Sturtevant's statement that the apparent third segment is in reality the missing arista was shown to be incorrect.

15. Knowledge as to the remaining members of the genus is briefly summarized, and a key to all the known species is given.

16. The history of the original introduction into California was investigated. It appears probable that two species, *iceryæ* and *monophlebi*, were introduced, but that only the former became established.

17. The economic importance of this insect was for a long while underestimated. It is potentially almost as efficient in the control of the Cottony Cushion Scale as *Vedalia*. The factors which go to make up this efficiency are discussed.

Bibliography.

Ayres, H. (1884.) On the Development of *Œcanthus niveus* and its Parasite *Teleas*. Memoirs Boston Soc. Soc. Nat. Hist. iii.

Berlese, A. (1913.) Intorno alle metamorfosi degli Insetti. Redia, ix.

Bezzi, M. (1919.) Nota sul Genere *Cryptochætum* con descrizione di una nuova species delle Filippine. Ann. Soc. Ital. Sc. Nat. in Milano, lviii. pp. 237–52.

Chamberlin, F. S., & Tenhet, J. N. (1926.) *Cardiochiles nigriceps*, an important Parasite of the Tobacco Bud-Worm. Journ. Agric. Res. xxiii. pp. 21–27.

Coquillet, D. W. (1889.) Insect Life, i. p. 377.

——— (1890.) *Ibid.* ii. p. 72.

——— (1890.) Pacific Rural Press, 27th December.

Eastham, L. E. S. (1925.) Peristalsis in the Malpighian Tubules of Diptera.... Quart. Journ. Micr. Sci. lxix. pp. 385–98.

——— (1929.) The Post-embryonic Development of *Phænoserphus viator*, Proctrypoidea Parasitology, xxi. pp. 1–20.

Embleton, A. (1904.) On the Anatomy and Development of *Comys infelix* Embleton, a Hymenopterous Parasite of *Lecanicum hemisphæricum*. Trans. Linn. Soc., Zool. ix. pp. 231–54.

Essig, E. O. (1922.) Journ. Econ. Entom. xv. p. 246.

——— (1926.) The Insects of Western North America. New York, p. 1035.

Fox, Munro. (1920–21.) Methods of studying the Respiratory Exchange in small Aquatic Organisms, with particular Reference to the Use of Flagellates as an Indicator for Oxygen Consumption. Journ. Gen. Physiol. iii. p. 565.

Frew, G. H. (1923.) On the Larval and Pupal Stages of *Forcipomyia piceus*, Ceratopogoninæ. Ann. App. Biol. x. p. 409.

Ganin, —. (1869.) Beiträge zur Erkenntniss der Entwickelungsgeschichte bei den Insekten. Zeit. Wiss. Zool. xix. pp. 381–451.

Hill, C. C. (1925.) *Platygaster hiemalis* Forbes, a Parasite of the Hessian Fly. Journ. Agric. Res. xxxii. pp. 261–75.

Howard, L. O. (1888.) Insect Life, i. p. 328 (note).

James, H. C. (1928.) On the Life-histories and Economic Status of certain Cynipid Parasites of Dipterous Larvæ, with Descriptions of some new Larval Forms. Ann. App. Biol. xv.

Keilin, D. (1915). Recherches sur les Larves de Diptères cyclorhaphes. Bull. Sci. Fr. et Belg. xlix. pp. 14–198.

KEILIN, D. (1917.) Recherches sur les Anthomiydes à Larves Carnivores. Parasitology, ix. pp. 324–450.

——— (1921.) On the Calcium Carbonate and Calcospherites in the Malpighian Tubes and Fat Body of Dipterous Larvæ. Quart. Journ. Micro. Sci. lxv. pp. 611–25.

KNAB, F. (1914.) On the Genus *Cryptochætum*. Insec. Inscit. Mens. Washington, ii. p. 35.

KRNUSCHER, E. (1922) Die Fettkorper und die Œnocyten von Dytiscus. Zeit. f. Wiss. Zool. cxix.

KUWANA, I. (1922.) Studies on Japanese Monophlebini. Dep. Ag. & Comm. Imp. Pl. Quar. St. Bulletin No. 2.

LEFROY, H. M. (1909.) Indian Insect Life, p. 632.

LUNDBECK, W. (1907.) Diptera Danica. See ii. p. 94.

MEIJERE, J. C. H. DE. (1916.) Studien über Sudostasiatische Dipteren.—XI. Tijd. voor Entom. lix. pp. 184–213.

——— (1925–26, etc.) Die Larven der Agromyzinen. Tijd. voor Entom. lxviii. pp. 195–293; lxix. pp. 227–317.

MELANDER, A. L. (1913.) A Synopsis of the Dipterous Groups Agromyzinæ, Milichinæ, Oethiphilinæ, and Geomyzinæ. Journ. New York Ent. Soc. xxi. p. 219.

MIALL, L. C., & TAYLOR, T. H. (1907.) The Structure and Life-history of the Holly-Fly (*Phytomyza*). Trans. Ent. Soc. London, pp. 259–83.

MUESEBECK, C. F. W. (1918.) Two important Introduced Parasites of the Brown-tail Moth. Journ. Ag. Res. xiv. pp. 191–206.

NASSONOV, N. V. (1910.) Untersuchungen zur Naturgeschichte der Strepsipteren. (German translation by Sipeagin & K. Hofeneder.) Berichte des Naturwiss.-medizinisch. Vereins in Innsbruck.

PANTEL, J. (1897.) Le *Thrixion halidayanum*. La Cellule, xv. pp. 1–290.

——— (1901.) Sur quelques détails de l'appareil respiratoire et de ses annexes dans les larves des Muscides. Bull. Soc. Ent. Fr. pp. 57–61.

——— (1909.) Recherches sur les Diptères à larves Entomobies. La Cellule, xxvi.

PARKER, H., & THOMPSON, W. R. (1925.) Notes on the Larvæ of the Chalcidoidea. Ann. Ent. Soc. Am. xviii. pp. 384–95.

QUAYLE, H. J. (1911.) Rep. Calif. Hort. Board, pp. 214–472.

RILEY, C. V. (1889.) Report of the Entomologist for the Year 1889. Washington.

RONDANI, C. (1875.) Species Italicæ Ordinis Dipterorum (Muscaria) Collectæ et Observati. Boll. Soc. Ent. Ital. Firenze, viii. pp. 168–69.

SILVESTRI, F. (1906.) Biologia del *Litomastix truncatellus*. Boll. Lab. Zool. Portici, i. pp. 1–51.

SKUSE, F. A. A. (1889.) Notes on the Genus *Lestophonus* (Will.), and Description of a new Species. Proc. Linn. Soc. New South Wales, 2nd ser. iv. pp. 123–26.

SMITH, H. S., & COMPERE, H. (1916.) Observations on the "Lestophonus," a Dipterous Parasite of the Cottony Cushion Scale. Month. Bulletin State Comm. Horticulture, Sacramento, Calif. v. pp. 383–89.

——— & ——— (1917.) Journ. Econ. Entom. x. p. 298.

SNODGRASS, R. E. (1924.) The Anatomy and Metamorphosis of the Apple-Maggot, *R. pomonella*. Journ. Agric. Res. xxviii. pp. 1–36.

SPENCER, H. (1926.) Parasites and Hyperparasites of Aphids. Ann. Ent. Soc. Am. xix. pp. 119–157.

SPEYER, E. R. (1929.) The Greenhouse Whitefly. Journ. Royal Hort. Soc. liv. pp. 1–12.

STURTEVANT, A. H. (1925–26.) The Seminal Receptacles and Accessory Glands of the Diptera, with special reference to the Acalyptræ. Journ. New York Ent. Soc. xxiii. & xxiv. pp. 196–215 & 1–21.

THOMPSON, W. R. (1928.) A Contribution to the Study of the Dipterous Parasites of the Earwig (*Forficula auricularia*). Parasitology, xx. pp. 123–58.

TIMBERLAKE, P. H. (1910.) Observations on the Early Stages of Two Aphidine Parasites of Aphids (*Praon, Aphidius*). Psyche, xvii. pp. 125–29.

——— (1912.) Experimental Parasitism. U.S. Dept. Agric. Bull. Tech. Ser. xix. pp. 71–92.

VAYSSIÈRE, P. (1926.) Contribution à l'étude Biologique et Systématique des Coccides. Ann. des Epiphytes, xi. pp. 197–382.

WILLISTON, S. W. (1888.) Insect Life, i. pp. 21–22 & 328–31.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Primary larva.
2. Second instar larva.
3. Third instar larva.
4. Third instar larva, tracheal system.
5. Fourth instar larva.

PLATE II.

Fig. 1. Third instar larva. Mouth-parts and sense organs of first two segments. *Ac.* Accessory sense organ. *Ant.* Antenna. *Mx.P.* Maxillary palp. *L.P.* Labial palp. *K.O.* Keilin's organ. *Ph.* Pharyngeal sclerite. *Hyp.P.* Hypopharyngeal plate. *Md.* Mandibular sclerite. *D.* Dentate sclerite.
2. Longitudinal section of anterior spiracle of fourth instar larva. *Cut.* Cuticle 1st post-cephalic segment. *Sp.* Spiracle. *At.* Atrium, or Felt-chamber.
3. Posterior spiracle of fourth instar larva, showing the branching of the main tracheal trunk to supply the tails. 10. Tracheal branches of 10th segment.

PLATE III.

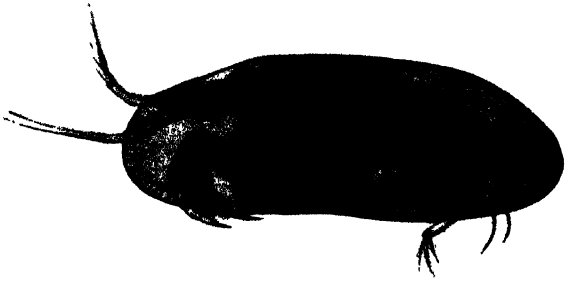
Fig. 1. Fourth stage larva. Bucco-pharyngeal apparatus, viewed from above. *D.* Dentate sclerite. *Md.* Mandibular sclerite. *Med.Dor.Scl.* Median dorsal sclerite. *Epi.* Epipharyngeal plate. *Hyp.* Hypopharyngeal plate. *Ph.* Pharyngeal sclerite.
2. Fourth stage larva. Bucco-pharyngeal apparatus, lateral view.

PLATE IV.

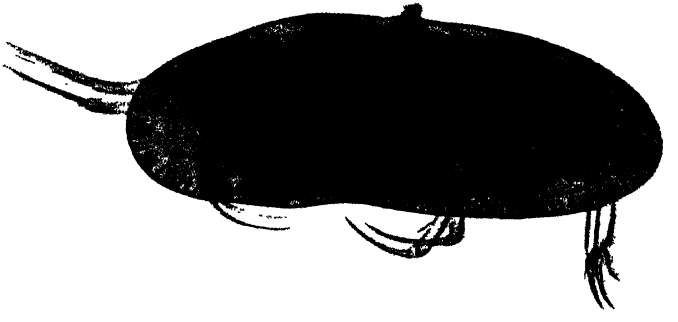
Fig. 1. Transverse section of tail of third instar larva, showing the large nuclei of the hypodermis and the six tracheæ. *N.* Nuclei of hypodermis.
2. Diagrammatic longitudinal section of part of tail of third instar larva, showing arrangement of longitudinal tracheæ. *Hy.* Hypodermis. *T.* Tracheæ. *Cu.* Chitinous cuticle. *B.* Lumen of tail containing blood.
3. Transverse section through base of posterior spiracles. *Sp.* Spiracle. *Sh.* Chitinous sheath. *Hy.* Hypodermis. *Cut.* Cuticle.
4. Group of œnocytes of fourth stage larva. *MT.* Tracheæ of the moniliform type. *T.* Tracheoles entering œnocytes and hypodermal cells. *Cu.* Cuticle. *Hy.* Hypodermis. *F.B.* Fat body.

PLATE V.

Fig. 1. Transverse section of posterior region of heart of last larval stage. *P.* Pericardial cell. *N.* Nucleus of heart-wall. *T.* Trachea. *H.G.* Hind gut.
2. Longitudinal section through junction of mid and hind gut of third stage larva, showing closure of mesenteron and the opening of the malpighian tubules into the proctodæum *Mes.* Mesenteron. *Mp.T.* Malpighian tubules. *Proct.* Proctodæum.



1.



2.



3.



4.



5.



6.

John Bale Sons & Danielsson, Ltd London

STENOCYPRIS MALCOMSONI BRADY.



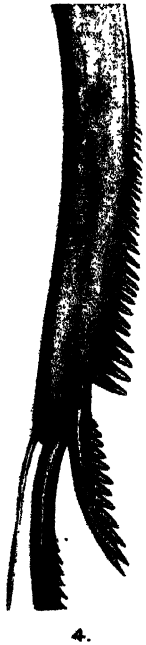
1.



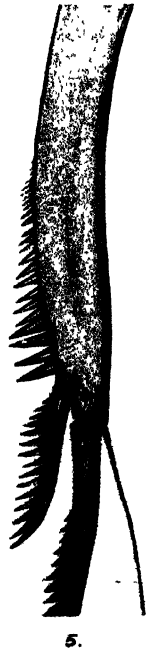
2.



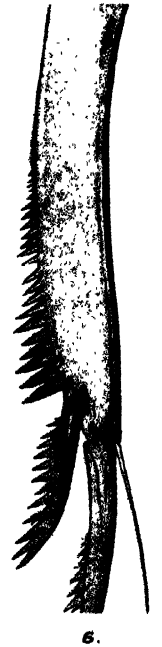
3.



4.



5.



6.

John Bale, Sons & Danielsson, Ltd. London.

STENOCYPRIS MALCOMSONI BRADY.

. . . from the New Hebrides collected by Dr. J R. Baker.

By A. G. Lowndes, M.A., C.M.Z.S.

[Received June 21, 1930: Read November 4, 1930.]

(Plates I. & II.*)

In 1927 Dr. J. R. Baker and a small party visited the New Hebrides, helped financially by a grant from the Percy Sladen Trust. A considerable amount of care was taken over the collection of Entomostraca in the large lake on the Island of Gaua. In addition two small samples of dried mud were brought back, and one of these proved to be of considerable interest. The lake in question is a large one, and over 300 feet deep. The pH at the surface was found to be 8·5 and the temperature 25° C. Considering the latitude of the island, 14° S., and its somewhat isolated nature, it might be expected that a rather specialized fauna would be found to occur.

The Ostracoda, Copepoda, and Cladocera have now been worked out and the results published, so that it is possible to make a brief survey of the whole and see how far this anticipation of a specialized fauna has been realized.

The following is a list of the species found :—

Ostracoda	*Stenocypris malcomsoni* Brady.
Cladocera	*Diaphanosoma sarsii* Richard.
	Alonella diaphana (King).
	Dunhevedia crassa (King).
	Chydorus sphæricus (O. F. Müller).
Copepoda	*Nitocra lacustris* Schmankevitch.
	Mesocyclops crassus Fischer.
	„ *obsoletus* Koch.
	Leptocyclops prasinus Fischer.
	Cryptocyclops bicolor Sars.

Also *Cryptocyclops anninæ* Menzel, but this species was not found in the large lake.

The Cladocera were examined by Miss P. M. Jenkin and recorded in 'Annals and Magazine of Natural History,' ser. 10, vol. iv. no. 21, p. 246 (Sept. 1929).

Only a few specimens of the Ostracod were obtained, and these were sent over to Dr. Klie of Bremerhaven. No report was published, but a statement was sent by Dr. Klie to Dr. Baker which said that the species was undoubtedly *Stenocypris malcomsoni* Brady; but it was not perfectly typical, since the individuals were rather larger and the caudal rami stouter and more coarsely toothed than usual.

I was entrusted with the investigation of the Copepods and also the mud.

The Copepods were identified and described in 'Annals and Magazine of Natural History,' ser. 10, vol. i. p. 704 (June 1928).

Distribution of the Species.

Stenocypris malcomsoni is a well-known species of Ostracod, having been recorded and described by Brady in 1859. It was fully described and figured by Sars in 1889. Sars obtained his specimens from dried Australian mud.

* For explanation of the Plates, see p. 977.

G. W. Müller in 'Das Tierreich' gives as the distribution India, Ceylon, Celebes, Australia, East Africa, and Sumatra. I have also received specimens from Dr. Klie from Austria; but these were probably obtained from dried mud, as they occurred apparently in something akin to hot-houses. Neither the species nor the genus is recorded as occurring naturally in the British Isles or in Europe. The species is, then, confined more or less to the Tropics and the East.

Of the Cladocera, *Diaphanosoma sarsii* is recorded from Australia, Sumatra, India, and Ceylon. *Alonella diaphana* is apparently confined to Australia. *Dunhevedia crassa* is recorded from Australia and South Africa. *Chydorus sphæricus* is, of course, cosmopolitan.

Of the Copepods little need be said. It is very curious that no Calanoid is represented while all five species of the other groups are well-known European species. All five occur in the British Isles and are practically cosmopolitan.

Summing up, then, we have ten species consisting of one Ostracod, four Cladocera, and five Copepods, and of these the one Ostracod is represented by an endemic variety, three of the Cladocera are restricted to the Tropics and the East, while of the five Copepods all are cosmopolitan. Or again the Ostracod and Cladocera are practically Australian while the Copepods are not.

Now there is nothing remarkable about the facts stated above taken by themselves, but when we come to examine them with our knowledge of their respective means of dispersal the result is rather extraordinary. Ostracods are known to possess resting-eggs. Many species, so far as is known, reproduce by parthenogenesis only, and actually the male of *Stenocypris malcomsoni* is unknown. The animals are very easily raised from dried mud, and yet their distribution is remarkably limited. For example, the commonest genus of temperate latitudes, *Candona*, is not recorded from south of the Equator. The Cladocera, in the same way, are known to possess resting-eggs and to produce parthenogenetically, and yet they are in many cases remarkably restricted.

When we turn to the Copepods the anomaly is truly remarkable. The freshwater Copepods are usually divided into three groups—the Calanoids, the Harpacticids, and the Cyclopids. In the Cyclopids resting-eggs are unknown with the possible exception of *Cyclops pictus* Koch. Sars raised cultures of Entomostraca from dried mud for years and obtained hundreds of species in this way; but only on one occasion did he obtain a single specimen of *Cyclops*. In addition to this there are two other cases on record. I have tried many times to obtain *Cyclops* from dried mud but without success. I have tried on several occasions the effect of taking mud from a pond with a large number of living Entomostraca and letting the whole dry up gradually in shallow dishes. On moistening the mud later I have always obtained Cladocera, Ostracods, and Calanoids (*Diaptomus*), but never *Cyclops*. What has been said about *Cyclops* is practically true about Harpacticids, though this group has received far less attention. Parthenogenesis has not been recorded among the Copepods, and in *Cyclops* it is very doubtful if it exists. I base my statement on the following observations. I have now at least six well-known species that I have bred from eggs up to the adult stage. In each case I have taken a number of females and separated them when I have known them to be in the virgin state. I have kept them isolated in many cases for over a month after they have attained sexual maturity. The result has always been the same, namely, that they have produced egg-sacs which have fallen off after a few days. The eggs have lain at the bottom of the vessel and there decomposed.

The Calanoids with their resting-eggs do not possess a single cosmopolitan species whereas many, if not the majority, of the species of *Cyclops* have a very wide distribution and are actually cosmopolitan.

So then one is faced with the fact that in the majority of cases where

every facility for distribution occurs the species is usually remarkably restricted, while in those cases where distribution seems most difficult the species are often cosmopolitan.

Stenocypris malcomsoni Brady (*raised from dried mud*).

As indicated above, Dr. Klie identified this species. I retained a specimen, but it it was damaged. The two samples of dried mud were placed in large jars and covered with Marlborough tap-water. One sample of mud was taken from the bottom at some depth, while the other was taken from much shallower water. The former yielded no Entomostraca, while the latter yielded a good culture of *Stenocypris malcomsoni*.

At the end of the year the culture was allowed to dry off and again wetted in the Spring, when another supply of the same Ostracod appeared. No males were seen, and in this respect the experiment agrees with the result obtained by Sars. The Ostracod therefore seems to reproduce entirely by parthenogenesis and the males are quite unknown.

Those familiar with Ostracods will realize that there is nothing exceptional about this particular Ostracod, for there are many genera, as well as species, of freshwater Ostracods in which the males have not been observed. It has been suggested that the males might be so small that they have escaped notice. This, of course, is not the case, for in *Stenocypris* alone there are several species in which the males are known, and they are never appreciably smaller than the females; in fact, it is exceptional among freshwater Ostracods for the males to be smaller than the females.

Again, there is another remarkable feature, and that is the relatively enormous size of the sperms, for the length of the flagellum of the sperm is usually of the nature of ten times the length of the adult Ostracod.

If, then, the males of the species in question are unknown, it would appear that the cultures of *Stenocypris malcomsoni* are of the nature of *pure line* cultures, and they should provide useful material for observing the effect or non-effect of environment.

Now, I took a specimen sent to me from Austria by Dr. Klie and one raised from dried mud from Gaua and photographed them side by side. Pl. I. fig. 1 is an adult animal from Austria, while Pl. I. fig. 2 is an adult animal from dried mud from Gaua. The only apparent difference is one of size. Fig. 3 represents the left caudal ramus of the Gaua specimen, while fig. 6 represents the corresponding limb of the Austrian specimen*. Fig. 4 represents the right caudal ramus of the Gaua specimen, while fig. 5 represents the corresponding limb of the Austrian specimen. All these limbs were photographed under exactly the same magnification.

It will be noticed that beyond the question of size there is little difference in detail. The shorter claw of both rami of the Austrian specimen are more curved than those of the specimen from Gaua, but, strangely enough, in this respect the Austrian specimen more closely approaches the specimens described by Sars from Australia.

Investigation of the Culture.

Now, having obtained a large number of specimens all belonging to the same species and to the same race, it was thought advisable to dissect a few and investigate the value of what was thought to be one of the chief specific characteristics.

Asymmetry of the caudal rami is one of the chief characteristics of the genus,

* The terminal seta was broken off in dissecting out the limb.

and the arrangement of the teeth on the rami and claws is considered the chief specific characteristic.

It was necessary to dissect a very few specimens to see that a considerable amount of variation occurred. The rami of three specimens were photographed under identical magnification, and the result is shown in Pl. II. Figs. 1, 2, & 3 represent the left ramus in each case, and it will be seen that the teeth of these rami show a considerable amount of difference. Fig. 2 shows the end of the ramus with teeth comparable in size to those of the claws. Figs. 4, 5, & 6 represent the right ramus of the same three specimens and the differences are just as pronounced.

Thus in fig. 4 the ramus shows coarse teeth at the end with a pretty regular gradation, the teeth becoming finer and finer along the ramus. In fig. 5 there are four equally coarse teeth, and the teeth do not extend back to the same distance along the ramus. In fig. 6 the ramus bears three coarse teeth, then two finer ones, and then another coarse tooth. The teeth are somewhat irregular but extend back further along the ramus.

Now these differences are trivial, but, at the same time, they are far more pronounced than many of the differences that have been used to separate species in other groups of Entomostraca.

As a result of this work one must conclude that too much stress should not be laid on such small differences in the genus *Stenocypris*, but the chief interest comes to light when one tries to consider the cause of these slight variations.

Suggested Cause of Variation.

It is obvious that the variation can hardly be attributed to environment, since all were bred under identical conditions so far as one can tell. Nor can these variations be of much value from the zoo-geographic point of view, for it would not be difficult to show that there is as much variation to be found among the individuals of a pure-line culture as there is between specimens taken from widely separated districts such as Australia and Austria or East Africa. I have also shown elsewhere that there is as great a difference to be found among the individuals of at least one species of *Cyclops*, taken from the same small pond, as there is to be found between individuals of the same species taken from widely separated districts.

Now recently there has been a great deal of attention given to the various causes of variation, and at the last Hooker Lecture the subject received considerable attention from Dr. E. J. Allen ("The Origin of Adaptations," Proc. Linn. Soc. 1928-29). Allen suggested that one of the causes of variation lay in the complex changes that took place during the process of cell division. "We cannot wonder that germ-cells thus produced differ in small repects among themselves. A few molecules more or less, a few atoms more or less, a few electrons even more or less, may mean changes in the offspring into which the germ-cell grows."

Now in putting this theory forward Allen gave these complex changes or processes as one of the causes of variation, but not as the only cause. But, still, if we accept this even as a possible cause we are driven to accept a far reaching corollary, and that is that in certain cases we must expect to see no correlation between variation and environment. It is true that these complex processes may be affected by external conditions, but they will none the less be complicated, whether external conditions remain constant or not, and it would seem to me that we are dealing with just such a case in the breeding experiments on *Stenocypris malcomsoni*.

In these breeding experiments the influence of any change of environment, in the commonly accepted meaning of the term, is eliminated, and we have

also eliminated such important factors as sexual selection and sexual dimorphism, to say nothing of the complications that normally may arise from copulation and the fusion of gametes etc. We are, in fact, driven to look for some cause that is not and cannot be correlated with environment, and it would seem that the complex processes taking place during cell-division offer the simplest and most likely solution to the problem. In allowing that one of the causes of variation lies in the dissolution and reformation of the chromosome complex, irrespective of external influence, one is open to the criticism that one is just relying on chance. This is, of course, perfectly correct, but one cannot deny the existence of chance nor disregard one's obligation of considering its effect.

Certain scientists have been severely criticized because they do not see how germ-plasm can be affected by soma, and therefore deny such effect. Their outlook is looked upon as being illogical, but is a total disregard of the existence of chance and its possible effect on the chromosome complex any more logical?

EXPLANATION OF THE PLATES.

PLATE I. *Stenocypris malcomsoni* Brady.

Fig. 1. Adult female from Austria.
2. Adult female raised from dried mud from Gaua, New Hebrides.
Figs. 3 & 4. Left and right rami respectively of the specimen from Gaua.
5 & 6. Right and left rami respectively of the specimen from Austria.

PLATE II. *Stenocypris malcomsoni* Brady.

Figs. 1, 2, & 3. Claws and tips of the left rami from three specimens of the culture.
4, 5, & 6. Shorter claws and tips of right rami from the same three specimens.

46. Notes on Stegocephalia and Amphibia. By Dr. Francis, Baron Nopcsa, C.M.Z.S., For. Memb. Geol. Soc.

[Received May 10, 1930: Read October 21, 1930.]

Although it is generally agreed that the Amphibia are somehow related to the Stegocephalia, the relationship has never been discussed in detail. The reason is that, until recently, the trend of evolution in the Stegocephalia was obscure. As Watson (**102**) has now, in a series of most important papers, elucidated the evolution of the Stegocephalia, and Noble and others (**71**) have determined the more primitive types among recent Amphibia, the problem of the relationship of the two groups can again be tackled.

That the recent Amphibia are a very old, but at the same time highly conservative, stock can be deduced from the occurrence of a highly specialized bufonid frog in the Como Beds of North America (**63**); a second, yet undescribed, splendidly preserved small frog—*Montsechobatrachus* Fejérváry, nomen nudum!—in the Kimmeridge rocks of Spain (**99**); and a third, fragmentary, pelobatid frog in the Tendaguru Beds of East Africa. Of the latter, two fused and well-preserved carpal bones are preserved, and these have been figured by Stremme (**93**) as metapodials of some Reptile, but they may in reality be carpals recalling those of *Macropelobates* (**72**). I propose to call the specimen *Stremmeia scabra* (nov. gen. et spec.). Of *Urodela*, one with functional gills (*Hylæobatrachus*) has been recorded from the Wealden of Belgium (**25**), and two without gills are known from the Cenomanian rocks of Italy. The latter have been described in an unsatisfactory manner by D'Erasmo (**23**). Among the other fossil Urodela, Meyer's *Polysemia* (**62**) and an unnamed specimen from the Tertiary rocks of Spain that has been figured by Sampelayo (**89**) in his work on the Fauna of Ribesalbes (fig. 63) deserve attention. Sampelayo's specimen recalls by its exoccipital process *Euproctus*. The skull, however, is broader than in any species of this genus. Apart from this the specimen is characterised by its very short body, consisting of 12 vertebræ carrying long ribs, of which the anterior are bifid, and with stout extremities. Evidently the specimen, which is exposed from the dorsal side, represents a primitive Urodelan and probably a *Tylototriton*, this genus being known also from the Miocene of Switzerland (**73**) *.

Watson (**103**) has shown that in the Stegocephalia the changes in the different phyla are always much the same and can be summed up as follows:—

1. The reduction or loss of the supraoccipital, basisphenoidal, prootic, and paroccipital bones.
2. The development of a strong parasphenoid, replacing the septum interorbitale and uniting more and more with the median branches of the pterygoids.
3. The extension of the exoccipitals over the auditory capsules.
4. The development of the tabular over the paroccipital and the union of the former with the exoccipital.
5. The extension of the epipterygoid.
6. The loss of the foramen for the hypoglossal nerve.
7. The breaking down of the ossification of the vertebral column, so that rachitomous vertebræ are formed, these only later on developing into the stereospondylous type.

* The Eocene *Ototriton* of Loomis has been determined by Gilmore (The Fossil Lizards of North America; Memoirs Nation. Acad. of Sciences, vol. iii. Washington, 1928) as an Amphisbænian.

In aquatic Stegocephalia, to these seven characters an eighth must be added, namely, the reduction of ossification in the primary cartilaginous scapular and pelvic arches, which is, however, accompanied in the scapular arch by an enlargement of the membrane elements of this region (clavicles and interclavicle or parasternum).

According to Hintsche and others (**46**), experiments on animals show that during ontogenetical development membrane bone continues to grow when subjected to an unusual strain, while cartilage continues to grow but fails to ossify. Thus, one might conclude that it was the unusual strain brought to bear, by terrestrial life, on the cartilage bones of the primitive Stegocephalians that led to their breaking down. Observations on other animals, however, show that such a hypothesis cannot stand.

About the same changes as those in the bones of Stegocephalia can also be observed in those of the marine Testudinata, for Turtles (**76**), and more especially *Dermochelys* (**69**), differ from the terrestrial Testudinata in the following points:—

1. The ossification is retarded in the basioccipital, the basisphenoid, and the otic region, and this retardation extends curiously enough even to the descending lateral flange of the parietal.
2. A strong parasphenoid is developed, which finally unites with the pterygoid, while the interorbital septum remains cartilaginous.
3. At the ends of the vertebræ much cartilage persists throughout life.
4. Much cartilage persists on the ends of the elongated bones of the shoulder-girdle, in which, in the middle, much periosteal bone is present, but even more persists in the place of the flat bones of the pelvis.

In the likewise aquatic Ichthyosaurians similar changes occur (**28**) but in a less marked manner. They consist in a certain lack of ossification in all the bones surrounding the foramen magnum and the ear, a reduction of the scapular and the pelvic elements, and the persistence of a certain amount of cartilage in the vertebral column. As in Stegocephalia, the clavicles are comparatively well ossified. The ossification of the membrane bones of the roof of the skull is not changed either in Testudinata or in Ichthyosauria; and in the aquatic Testudinata these bones even show a tendency to grow.

Even in the Plesiosaurians the otic region is less ossified than in the Nothosaurians, which must be considered as their predecessors (**97**).

This distribution of cartilage and bone in highly aquatic animals is quite different from that observable in those Dinosaurs in which the pituitary fossa is enlarged. In these, the lack of ossification is exclusively restricted to the ends of the limb-bones, while the otic region, the base of the skull, the scapular arch, and the pelvis, ossify in a normal manner even in those types that were semi-aquatic (**77**) as the Sauropoda *.

* In a recent paper ("Die fossilen Gehirne," Ergebn. d. Anatom. u. Entwicklungsgesch. iii. Abt. der Zeitschr. f. gesammt. Anatom. vol. xxviii. Berlin, 1929), T. Edinger expresses the view that the gigantic size of several Dinosaurs is not in causal connection with the large size of their pituitary fossa. It is true that the size of this fossa alone is no argument for such a connection. When one considers, however, that the difference of the internal structure of the limb-bones and vertebræ is much greater in the large Dinosaurs than in their smaller relatives, and that the hyperfunction of the anterior part of the hypophysis augments this difference also in recent Mammals (the internal structure of the femur of acromegalic giants is exceedingly coarse), then the problem assumes another aspect. Apart from this, Edinger does not seem to distinguish the gigantism that frequently follows castration clearly from that due to pituitary disturbance. Edinger's hypothesis that during the Cretaceous period something must have existed that forwarded growth in general ("dass das Kreidemilieu irgendwelche wachstumfördernde Stoffe bot"), can be definitely refuted by the observation that, during the time that the European Titanosaurians were small, the South American Titanosaurians grew to enormous size. Huene mentions, from South America, a femur 2 metres in length! (Fr. von Huene Los Saurisquios y Ornitisquios del cretaceo argentino; Anales del Museo de La Plata, vol. iii. (ser. 2), Buenos Aires, 1929). This case excludes even the hypothesis that the enormous size of these animals can be explained by the coincidence of the Equator and the Ecliptic during the middle of the Mesozoic, by which all seasonal changes disadvantageous to development were eliminated.

Considering all this, probably even the reduction of the embolomerous vertebræ to the rachitomous type, and the subsequent development of stereospondylous vertebræ in the Stegocephalia fall within the limits of the changes established for aquatic animals. Watson (**104**) describes each half-vertebra of an embolomerous vertebra as consisting of a double cone of dense bone surrounding the continuous notochord and itself surrounded by a ring of cancellous bone with an external layer of compact bone. This description shows that each half-vertebra of an embolomerous Stegocephalian corresponds to one entire chondrogenous vertebra of a Selachian, differing only by being covered with a thin layer of periosteal bone. Thus, in the Stegocephalia the development of the holospondylous type from a rachitomous or phyllospondylous vertebra would mean nothing more than that, first, the primitive cartilage ossification (embolomerous type) of the vertebral column broke down leading to the formation of thin vertebræ of periosteal bone (phyllospondylous and rachitomous types), and that then this type was strengthened so as to form holospondylous vertebræ (pseudocentral, notocentral, gastrocentral type). Perhaps one may mention, as an analogous phenomenon, that after bone-fracture in Amphibia first a callus of cartilage is always formed, uniting and fixing the broken bones, and that only later periosteal bone is formed, while the callus ossifies, or is resorbed. In Mammals frequently, likewise, cartilage is first formed; sometimes, however, the formation of membrane bone sets in at once (**119**).

The fact that Osteolepida have no cartilaginous vertebral ossifications cannot be brought forward as an argument against this explanation of the evolution of the vertebral column, for evidently even the ossification of the cartilage in this region was only stimulated when terrestrial life began.

Unfortunately, it is not yet known how aquatic life can act on the ossification of cartilage bone. As, however, the disturbance in bone-formation caused by aquatic life is exactly the same as that caused by the defect of thyroid hormone (**60**), so, perhaps, a correlation exists between these two factors*. To prove the resemblance of the two sorts of changes it is enough to point out that, in human pathology also, the deficiency of thyroid hormone affects the ossification of cartilage, while it does not affect the long bones. Thus, this defect retards the ossification of the epiphyses, of the carpals and tarsals; moreover, it affects the development of the basicranial bones, leading thus, as in Cetaceans, to a shortening of the basicranial axis, to deeply lying eyes, and to a saddle-shaped nose; while, on the contrary, the bones of the cranial roof bulge out in an abnormal manner, for these membrane bones develop to normal or nearly normal size. Professor O. Abel has kindly pointed out to me that, in Cetaceans especially, the ethmoid bone is shortened, as is the case in thyroidless cretins, and it is evidently this shortening of the basis cranii that leads in these animals both to the curious overlapping (telescoping) of the membrane bones of the skull (**57**) and to the shifting of the nares. As a minimal shifting of the nares backwards cannot have been of any use in the Cetaceans, and as in *Physeter* the exterior nasal opening is always still at the anterior end of the skull, primarily the shifting of the nares backwards can evidently not be exclusively due to the requirements of breathing. Frequently in Cetaceans the disadvantageous frontal concavity brought about by the shifting of the nares and the abbreviation of the ethmoid is neutralised by bony excrescences (*Platanista*), or filled up with tissue (*Physeter*), so as not to spoil the flow-line of the body of the animal.

The same normal or nearly normal development as in the membrane bones of the skull can also be traced in the development of the periosteal parts of the "long

* If the ossification were retarded equally in *all* bones of marine Vertebrates, one might be inclined to explain it by the retarding influence of Magnesia and NaCl on ossification, but this is not the case (Kramer, Shelling, & Orent, "Studies upon Calcification *in vitro*," Bulletin, Johns Hopkins Hospital, vol. xli. 1927).

bones" of cretins, except that the structure of these parts becomes somewhat dense (24). This change is likewise known to occur, sometimes even in an excessive manner, in aquatic animals, but hitherto it was supposed to be due to other factors than hypothyroidism (78).

How complicated the question is, may be gathered from the correlation that Ascher (2) believes he has detected between the spleen, the bone-marrow and the thyroid gland. Regarding the connection between air-supply, bone-marrow, osteosclerosis, and aquatic life, reference may be made to a former paper (78), in which this connection was suspected: and later on the experiments of Mark (61) showed that connections between the air-supply and the thyroid actually exist. It is true that in 1923 the rôle of the red blood corpuscles had not been suspected. All this goes to show that a prolonged stay in water may have an effect on the parts regulated by the thyroid gland (79). Other observations incline to strengthen this view.

Especially in cases of maniacal and paralytical excitement, but even in cases of delirium tremens, a continuous stay in warm water, prolonged for several days or even weeks, has a powerful quietening effect, leading even to sleep, and causes a dilatation of the blood-vessels of the skin and a lowering of the blood-pressure (59). Just the same sort of tremor as in these nervous diseases is present in cases of hyperthyroidism (Basedow disease), and as hyperthyroidism goes with an irritability of the vasodilatatorial nerves, an acceleration of the metabolism, with sleeplessness and a more or less pronounced maniacal alteration of character; hypothyroidism, on the contrary, is accompanied with sleep, apathy, and a lowering of all metabolic processes (3), so in some manner or other, a prolonged stay in water acts similarly to hypothyroidism. Professor Gaupp in Tübingen kindly informed me that, unluckily, hitherto nothing is known about the question, whether in such cases of excitement a prolonged stay in water affects the metabolism of the body. Delcourt-Bernard and Mayer, however, showed in a joint paper (22) that a stay in water of 36° C. affects metabolism even in healthy individuals. Apart from this the researches of Vogt (100) and Harpuder (37) likewise tend to show that a correlation exists between the endocrine glands, the vegetative nervous system, and the effects of water which is more or less rich in dissolved substances.

All this shows, that it was at least premature when Fries stated (29), in spite of all contradicting palæontological evidence, that a prolonged stay in water can have no effect on the structure of bone.

To all this the strongly dehydrating effect of the thyroid hormone has also to be added (4), and the observation that the average percentage of water is comparatively high in the tissues of lower Vertebrata.

Perhaps this is the place to mention that the growth of the body of a tadpole is to a great extent due to its taking up water, while the growth of its extremities, therefore those parts that are under thyroid-control, is due to cell-division. The growth of the chicken in the egg is also accompanied by a loss of water, so that the weight of a newly born bird is always about two-thirds of the weight of the egg. This uniform desiccation, that is independent of the proportion of yolk and albumen in different sorts of eggs, also explains why in many Reptiles and the nidifuge birds, in which the young are born in a very developed state, the amount of yolk is comparatively greater than in the nidicole birds, that are less developed at birth. In the nidifuge birds the average percentage of the yolk is 33 per cent., in the nidicole birds only 18 per cent., in Tortoises and in Crocodiles 40 per cent. (42). Moreover, the percentage of water is smaller in the yolk than in the albumen, being on the average only 49 per cent. in the former, but 85 per cent. in the latter (58) *.

* According to the description of the crocodilian egg given by Voeltzkow ("Biologie und Entwicklung der äusseren-Körperform bei *Crocodilus madagascarensis*" Abhandl. Senckenber. Naturforsch. Gesellsch. Frankfurt; 1899) the albumen of the crocodile egg seems to contain even less water than the albumen of a bird's egg.

That the thyroid gland of the primitive aquatic Vertebrata had been greatly affected, when they passed from aquatic to terrestrial life, has already been supposed by some authors (**27**), and it is therefore quite logical to suppose that this was also the case when they became adapted again to this environment. Palæontological research seems to show that the metabolic disturbances of the secondary adaptation to water gradually diminished, for in the most specialised aquatic Tetrapods (Cretaceous Ichthyosaurs and Plesiosaurs) all cartilaginous parts such as their carpal and tarsal bones, as well as the bones of their shoulder-girdle and pelvis, are again quite well ossified (**80**). How this is brought about will be discussed in detail on another occasion. The processes that seem to be important have already been alluded to in a previous paper (**79**).

Without thyroidectomy in Amphibia neoteny can also be artificially produced by simply rearing these animals in relatively cold water, for this prevents the thyroid gland from acting in a normal manner (**74**). Hesse (**43**) has brought many cases together showing how maturity is postponed by the influence of cold, while the body continues to grow, and even the healing of bone fracture is retarded in cold-blooded animals by cold (**120**). Thus it might be supposed that the breaking down of the ossification in Stegocephalia was due to the lowering of the temperature at the end of the Carboniferous that finally led to a great ice age, but such an explanation cannot account for the analogous changes in the rest of the aquatic animals.

Turning now from the extinct animals to the present Amphibia, Watson has shown (**103**) that they evolved parallel to the Stegocephalia, so that in the Amphibia the cartilage bones of the skull also became reduced. In many of the more aquatic Urodela the pelvic ossification is also retarded, but, apart from this, in the Amphibia several of the bones of the roof of the skull became smaller. The structure of the roof of the skull of the recent Amphibia can only be derived from a Stegocephalian skull in which two temporal vacuities opened. This hypothetical formation of temporal vacuities in the Amphibia can well be compared with the similar changes in the skulls of primitive terrestrial Reptiles, for both changes are paralleled by the observation that, during terrestrial life also, the plate-like scapular and pelvic elements are gradually turned by fenestration to more or less rod-shaped bones (fenestration in Nothosaurians, Crocodiles, Tortoises, Lizards, and Dinosaurs (**80**)). The occurrence of a fenestration in Jaekel's *Gephyrostegus* (**53**), that evidently differs by the structure of its vertebræ from Watson's *Diplovertebron* (**104**), actually represents a Stegocephalian type in which temporal vacuities are just appearing.

One of the temporal vacuities of the Amphibia seems to have opened between the parietal, the tabular, and the squamosal and to have led to the formation of the temporal bar, which can be seen in all the primitive Urodela, as *Polysemia*, *Euproctus*, *Pleurodeles*, *Palæotriton* (**8**), etc.; the other vacuity is shown in the Anura In the Urodela this second vacuity evidently united with the orbit.

The reason why the lower vacuity, which vanished in the Urodela, persisted in the Anura is obvious. Starting from the evidence afforded by all unspecialised Reptiles, that the primitive position of the suspensorium mandibuli was the one in which this part joined the mandible about at a right angle, both the rotation of the suspensorium forwards and the rotation backwards must be considered as cases of specialisation.

A backward rotation occurs in some Urodela as *Euproctus*, *Cryptobranchus*, and *Hynobius* (**8**), more or less in many Anura (**7**), in many Stegocephalia, in the carnivorous Cotylosaurian *Labidosaurus* (**105**), in the carnivorous Pelycosaurians (**16**) and Plesiosaurians (**1**), in the Viperid Snakes, and in most Crocodiles. In the embryos of Snakes (**87**) and Crocodiles (**65**) this rotation sets in during this ontogeny. This synopsis shows that the backward rotation occurs in all animals in which a wide gape of the mouth and a rapid opening, as well as a rapid

subsequent closing, are of great importance. This is attained by a backward rotation, because in such a case the mandible forms a longer lever. As the pressure brought to bear against the articular surface of a quadrate rotated backwards is not taken straight up by the bone, but tends to turn the bone still more backwards, naturally in nearly all these cases a strong connection of the quadrate with the anterior part of the skull becomes of great importance. This connection can either be brought about on both sides of the skull by the quadratojugals and jugals or near the median line by the pterygoids and the vomers. The embolomerous Stegocephalia, the Anura, the Plesiosaurs, and the Crocodiles may all be quoted as examples in which the union is brought about by the jugal (and quadratojugal) bar, and in Plesiosaurians even a secondary strengthening of this bar can be detected. In the Cretaceous forms *Cimoliosaurus* and *Dolichorhynchops* the jugal bar is stronger than in their respective Jurassic predecessors *Plesiosaurus* and *Peloneustes*. Pelycosaurs are an instructive case, in which the quadrate is prevented from rotating unduly backwards by the pterygoids, while in the specialised Snakes the muscles closing the mouth have such an arrangement that some of them pull, when constricting, the quadrate forwards (**35**).

Quite another structure is met with in those Amphibia and Reptiles in which a wide gape of the mouth is not essential and in which the jaws perform slow but sometimes powerful work. In such animals the quadrate is rotated forward. This type is met with in the neotenic Amphibia. (**112**) as *Amphiuma*, *Proteus*, *Siren*, *Menobranchus*, in the herbivorous Diadectids (**17**), the Pareiasurians (**105**), the short-snouted herbivorous(?) Dinocephalians [example: *Mormosaurus* (**106**)], in the edentulous Dicynodonts (**13**) and Testudinata (**9**), in the likewise edentulous *Struthiomimus* (**84**), that originated from a carnivorous type (!), in all herbivorous *Sauropoda* (**116**) and *Ceratopsia* (**85**), in the frugivorous and insectivorous *Nodosauria* (**33**), and in the Pterosaurians (**48**). Apart from these the same modification of the quadrate is observable in the burrowing forms such as *Ichthyophis* (**90**), Amphisbænidæ (**32**), *Anniella* (**20**), Rhinophidæ (**6**) and the Angiostomatid Snakes.

In this type of rotation two modifications of the quadrate are recognisable. When the jaw is principally closed by the aid of the pterygoid muscles, which lie far in front of the upper end of the suspensorium mandibuli, the anterior and superior borders of the quadrate are generally applied against some other bone (examples: *Menobranchus*, *Siren*, *Struthiomimus*, *Pteranodon*); when, however, the closing of the mouth is done by the masseter, which runs upwards and backwards and thus parallel to the suspensorium, a mere thickening of the quadrate is enough to bear all the pressure. As examples for this second type one can quote: *Gymnarthus* (**49**) *Lysorophus* (**92**), *Neotriton* (**8**), *Amphiuma*, *Mormosaurus*, *Typhlops*, and Tortoises. In all these animals a lower arch is more or less absent; a strong coronoid process is, however, present. Thus one may not attribute to the arches of Amphibia a too great phylogenetic importance; they show, however, quite clearly, that even the recent aquatic Amphibia are derived from a terrestrial stock. Hoffker (**47**) recognised this already when studying the columella auris of *Archegosaurus*.

Other characters of the Amphibia that need mentioning in this paper are: (1) the coarse granulation of the dermal bones in many Urodeles, (2) the intermaxillary gland, (3) the small bone attached to the exoccipital process in *Siren*, (4) the balancer organs of Cœcilians, of the larvæ of some *Urodela* and of the larva of the frog *Xenopus*, (5) the arciferous sternum and the opisthocœlian vertebræ of the Urodela and of the relatively primitive or quite primitive Anura, (6) the scales of the Cœcilians.

The intermaxillary gland occurs in nearly all Amphibia and secretes a sticky substance by which the prey adheres to the tongue. This gland is located in a perforation in the middle of the skull and is, of course, especially well developed in

terrestrial forms. It is more or less reduced in the aquatic newts (8) and perfectly in Cœcilians and neotenic Amphibians. For palæontologists it is, of course, of great importance to distinguish those skeletal modifications that are brought about by this gland from those that result when the internarial septum becomes visible on the surface of the skull. The latter case is recorded in the Cœcilians *Siphonops* (11) and *Boulengerula* (86), and in the Stegocephalians *Osteophorus* (11), *Ricnodon* (107), *Eryops* (11), *Kestrosaurus* (38), and *Trematosaurus* (39)*. All these Stegocephalians belong to a well-defined natural group, in which *Eryops* represents the most primitive type (103).

The distribution of the internarial perforation among the Stegocephalia is quite different from that of the median septal bone. As in Amphibia, so also in Stegocephalia, the internarial vacuity is always situated at the place where the naso-maxillary suture crosses the median line of the skull. The size of the aperture varies. It is small in "*Melanerpeton*" *pusillum* (30) and in *Micropholis Stowi* (107), but large in *Acanthostoma vorax* (54), *Dasyceps* (50), and *Zatrachys* (14). In *Trematops* it is sometimes present but sometimes closed (113). As this aperture is at the place where the primitive embolomerous Stegocephalia have the "internarial bone" (108), so perhaps the small ossicles visible in the internarial opening of *Micropholia* (107) are the last traces of these ossifications. This would account for the closing of this opening in the more primitive species of *Trematops*, for *Trematops* and *Micropholis* seem to form somehow a natural group. This group is characterised by the presence of a turbinal bone, by enormous interpterygoid vacuities, and by a strong reduction of the parasphenoid.

Acanthostoma, *Dasyceps*, and *Zatrachys*, in which the internarial opening is always large, form likewise a natural group. This second group is characterised by a curious "spiny" modification of the squamosal region, which terminates in two pronounced flanges, and by hornlike projections of the tabularia. To the animals clustering round *Zatrachys* evidently *Platyhystrix* (114) has also to be added, although the internarial region of this Stegocephalian is still unknown. Huene (50) was the first to point out that the internarial vacuity of the Stegocephalia probably lodged an intermaxillary gland. Contrary, however, to his opinion, that this organ is of small value in the classification of the Stegocephalia, I would rather lay a certain amount of stress on its systematic value. It is true that when Huene made his statement, Watson's papers had not yet appeared.

Quite recently Romer (88) pointed out that *Stegops*, in which an internarial aperture is still missing, may be ancestral to this group. It seems therefore that this group evolved from an aquatic type and culminated in the large terrestrial Permian *Dasyceps*.

Even the scarcity of remains of *Dasyceps*, when compared with the rather frequent occurrence of other large Permian and Triassic rachitomous and stereospondylous Stegocephalians, indicates that this genus was comparatively terrestrial, so that its remains had less chance of becoming buried in material deposited under water.

Wiman (117) does not accept the view endorsed by Huene, for in a Triassic Stegocephalian he studied, the intermaxillary cavity is filled by cancellous bone, which leads him to believe that this lacuna represents an unossified part of the ethmoid region. As it is, however, quite likely that the intermaxillary gland is obliterated in such a highly specialised marine genus as *Tertrema*, his arguments do not seem conclusive. In the group leading from *Acanthostoma* to *Dasyceps* the size of the intermaxillary opening is too large and too persistent a character to be due only to a lack of ossification.

The vertebræ of *Acanthostoma* (21) are either holospondylous or phyllospondylous, those of *Platyhystrix* (115) are stereospondylous, those of *Zatrachys* and *Dasyceps* are unknown. From the vertebræ of all Stegocephalia, those of *Platyhystrix* differ

* *Trematosuchus* is considered to be generically identical with *Trematosaurus*.

by a very great prolongation of the neural spine. A similar prolongation, but of smaller degree, is found in a Cotylosaurian, *Dispuractus* (18), in a more marked manner in many Pelycosaurians (34) as *Clepsydrops* and *Dimetrodon*, in the Naosaurians (18), in some Iguanid and Chameleonid Lizards, and in some Dinosaurs (94). This character is therefore not rare in lower Vertebrata, but it occurs *only in terrestrial types*. It can only to a certain extent be compared with the support of the sexual ornament in some aquatic Tritons, for in the latter the support of the filament forming the sexual ornament is not built up by bone but by intumescent blood-vessels (8), so that the filament is erected in the same manner as the ornament in many birds (118).

That the balancer organs of Cœcilians should be alluded to in a paper dealing with Stegocephalia may seem rather strange, but as these organs are present in the larvæ of some Urodela (as *Hynobius*, *Amblystoma* (68), and *Salamandra* (66)), and as they are also present in the larvæ of the primitive Frog *Xenopus* (70), they seem to be of phylogenetic importance. Sarasin (90) observed in *Ichthyophis* that the tentacles were used for feeling, and as they are reduced in the larvæ of those Urodela that inhabit swift running and thus clear water, while they are present in those inhabiting stagnant and thus more or less muddy water (75), so probably their function in the Urodela is much the same as in the Cœcilians. Nikitin (70) showed that this is also the case in the larvæ of *Xenopus*. In these the tentacles are, nevertheless, provided with blood-vessels and nerves; in the larvæ of *Hynobius*, however, both are already wanting. The difference in the development of the retractile tentacles of the Cœcilians and the non-retractile tentacles in the other Amphibia, can easily be explained by assuming that it was for the former of utmost importance to have these organs protected while digging with the head. Accordingly, in the Cœcilians the tentacles are implanted in two deep fossæ between the orbits and the nares.

As *Zatrachys* is the single Stegocephalian in which there is a deep pit or depression between the orbit and the nares (14) that might have lodged a tentacle, this feature is important, for the presence of such a tentacle would be well in accordance with the terrestrial mode of life of this genus as inferred from the shape of the neural spines of a close relative.

Apart from the occurrence of an intermaxillary gland and of tentacles (balancers) both in Urodela and Anura, for the question of their origin, the posterior exoccipital projections of *Euproctus* [called by Bolkay (8) paroccipitalia] are also of no small importance. Similar projections occur in *Siren*, though in this genus their ends bear small isolated bones (112). In the Stegocephalia posterior projections of the skull occur in several genera. Formed by the tabulars, they are well developed in the embolomerous *Palæogyrinus* and *Eogyrinus*, and seem to have touched in these, as in fishes, the superior end of the scapular arch (104). They are, moreover, present in *Acanthostoma*, *Zatrachys*, *Dasyceps*, and *Platyhystrix*, in which they are likewise formed by the tabular bones, and the great lateral horns in *Diplocaulus* (26), *Batrachiderpeton* (109), *Diceratosaurus* (55), and *Keraterpeton* (110) are likewise formed to some extent by the tabulars, but in the latter genera the squamosals are also elongated and join the tabulars. *Cochleosaurus* (12) has small posterior projections that are formed by the exoccipital bones. As the projecting ossicles are borne in *Siren* by the exoccipital bones, one may take these ossicles to be reduced tabulars that have evolved from a *Zatrachys*-like stage.

A study of the vertebral articulation of the Anura is still more interesting. It has been pointed out in a previous paper, that in all Vertebrata having convexo-concave vertebral articulations the concave surface is always directed so that its concavity looks towards the relatively stable part of the body (81). In accordance with this, the Urodela, in which the anterior extremities develop before the posterior ones, have opisthocœlous vertebræ, while the majority of the Anura have procœlous vertebræ, for in these the posterior extremities develop sooner. The few

Anura in which opisthocœlous vertebræ occur, were, in accordance with the views of Noble (71), considered as primitive, and *Megalophrys* was considered as a transitory type, in which the condyles were already detached from the anterior ends of the following vertebræ, but not yet united with the ends of the preceding vertebræ. That this is the right explanation of the procœlian vertebral articulation of most Anura may be deduced from the observation that in one of the few opisthocœlous Frogs, *Liopelma*, even the anterior extremities develop, as in Urodela, before the posterior (75).

This and the preceding characters all show that the Amphibia must have developed from a leptospondylous, Salamander-shaped form, in which an opisthocœlous, but perhaps cartilaginous, vertebral articulation had been attained. In this form the cranial roof must have had two pairs of openings, the palate a widely dispersed dentition, while an intermaxillary gland and tentacles were present. This shows that this form was terrestrial, but it must have originated from an aquatic form in which the cartilage bones had become reduced.

Unfortunately, nothing is known of the dermal cover of most Stegocephalians; several, however, that come near to the Carboniferous *Acanthostoma* have rounded scales (21) like the recent Cœcilians. The structural resemblance of the scales of *Discosaurus* to those of the Cœcilians was emphasised by Credner. Thus we may suppose that the ancestor of the Amphibia was also clad with rounded scales. Hence we may look for this ancestor among the Stegocephalia, and it probably was, as Moodie (64) pointed out, allied to the Branchiosaurians. These had, like the modern Amphibia, a metamorphosis, though it was less pronounced than in the recent Amphibia. Thus one comes to the curious conclusion that the divergence observable between the larvæ and the adults of Amphibians is a character that is augmenting in the course of evolution. An analogous case can be observed in Insects, for in these also the divergence between the larva and the imago is greater in the more specialised types (Coleoptera, Lepidoptera) than in the primitive Orthoptera. In both cases the divergence is brought about by the retrograde adaptation of the larva, that recalls, in the higher Insects, in a general manner a Worm, while it has, in the Anura, a certain resemblance to the larva of some *Tunicata* (sucking disc, egg-shaped body, long tail).

Taking the relationship of the Amphibia and the Branchiosaurian for granted, and also bearing in mind that a related type, *Acanthostoma*, has the same tabular process that one still finds in *Siren* and Urodela, that *Acanthostoma* has a well-developed and extensive dentition on the palate, an intermaxillary gland, the vertebral structure of an Amphibian, and that it was more or less terrestrial; lastly, that *Zatrachys*, a specialised descendant of *Acanthostoma*, had perhaps even a balancer organ (tentacle), one may presume that *Acanthostoma* is very near to the origin of the Amphibia. It is not improbable that the Cœcilians branched off very soon from the form that gave rise both to the Urodela and Anura (98), but this question demands yet further consideration.

Having thus dealt with the origin of the Amphibia, we may now consider why they could not compete later on with the Reptiles. The nature of the sediments in which the remains of Stegocephalians occur gives the answer (19). In the boggy deposits represented by the Kilkenny Coal beds, by the Linton Coal beds, the Nova Scotia Coal beds, and the Nyrsan Coal beds, Branchiosaurs and other aquatic newt-shaped Stegocephalians (*Nectridia*) dominate, eel-shaped Stegocephalians (*Aistopoda*) are not infrequent, and some larger embolomerous Stegocephalians are met with, and the latter were probably semi-terrestrial, for their head is not at all depressed.

In the former mud-deposits (shales) of Mazon Creek, the limestone of the Döhlen Basin and of the Sudetic basin, Branchiosaurs always predominate, and Crocodile-shaped Archegosaurians are met with, but at some places one or two larger semi-terrestrial Stegocephalia allied to *Eryops* already occur. In these places,

moreover, remains of different terrestrial Reptiles are intermingled with the Stegocephalia. In the shales of Autun the fauna is much the same.

On the other hand, in the Red Beds of the Wichita series, which were deposited in a dry climate, and in the limestones and shales of the Clear Fork group (**18**), apart from a few aquatic animals such as *Lysorophus* and *Diplocaulus*, various short-limbed and short-tailed, therefore more or less terrestrial, Stegocephalians, such as *Eryops* and *Trematops* and shielded Cacopsidæ, are chiefly met with, but Reptiles are even more abundant. The rapacious Reptiles are mostly Pariotichidæ and Pelycosaurians, the herbivorous forms Diadectidæ. In the more or less semi-arid sandstone of Elgin the Pelycosaurians have already nearly vanished, and small Dicynodonts and Pareiasaurians appear. The fluvial sandstones of the Dvina contain a fauna in which only a few highly modified, flat-headed, and short-limbed Stegocephalia occur and Reptiles dominate. The rapacious forms are represented by comparatively swift Therocephalians and Gorgonopsians, the herbivorous forms by large Pareiasaurians and large Dicynodonts. This shows that the Dvina beds contain about the same fauna as the South African Endothiodont Zone (**40**), while the poorly known fauna of the fluvial copper-sands of the Ural region, in which some large Stegocephalians are found with Dinocephalians, correspond to the South-African *Tapinocephalus* Zone (**82**). Haughton (**41**) supposes that the climate of the *Tapinocephalus* Zone was comparatively damp, but for the following *Endothiodon* Zone he and Huene (**51**) assume that it is an accumulation on dry land. It is only for the Upper Beaufort beds that both authors again assume a moister climate. In accordance with this both in the Lower and Middle Beaufort beds only two genera of Stegocephalia were discovered, while the Upper Beaufort beds yielded nine (**38**). Most of these are also known from the Lower Triassic of Europe, and with the exception of *Micropholis* they all belong to the large-headed labyrinthodont type with small extremities but an enlarged membrane shoulder-girdle (**103**).

This rapid review shows that the primitive Stegocephalia were limited to marshy or even boggy places, that later on quadrupedal more terrestrial forms (Eryopsidæ and Cacopsidæ) developed, but that these later on again returned to a more or less aquatic life (Labyrinthodonts). The primitive Branchiosaurians were endowed with reptilian scales and therefore probably suffered less from the dryness of the climate than modern Amphibia; on the other hand, the geological record shows that the Stegocephalia could not compete with the Reptilia during the desiccation of the climate between the Carboniferous and the Lower Trias, and their extinction was probably brought about by the climatic change, but evidently it was not due to the structure of their skin.

Noble (**75**) and Sarasin (**90**) have pointed out that in the Cœcilians and in all the aquatic Urodela the eggs are surrounded with two coats of albumen, of which the inner is secreted by the oviductal glands, while the outer is secreted by the cloacal glands. Contrary to this in terrestrial Amphibia the cloacal glands are absent (**75**), and so there exists also no outer layer of albumen. In birds and reptiles the albumen is likewise formed in the upper part of the oviduct, but to this albumen layer in the lower part of the oviduct an outer layer of lime in Tortoises (sometimes arragonite) is added (**31**) forming a layer of sphærocrystals of varying thickness and of varying cohesion (**91**).

As in thyroidectomised hens the shell of the egg is much thinner than normally (**15**), and as the complete ossification of bone-fractures takes a much longer time in Urodela than in Anura or Lizards, and in these, again, a longer time than in small Mammals or Birds (**101**), it seems as if the whole metabolism of lime must be faster in a higher animal than in a lower *.

* Regarding the relation of the thyroid gland to Calcium metabolism in general, see the papers of J. C. Aub ("The Relation of the Thyroid Gland to Calcium Metabolism," Trans. Assoc. Amer. Physicians, vol. xlii; Philadelphia, 1927) and F. S. Hammett ("Studies of the Thyroid Apparatus," part xxvii.; Journal of Metabolic Research, vol. v.; Morristown 1924).

How far such an augmentation of the calcium metabolism might account for the development of excrescences (spines, crests) in the very strongly specialized members of different groups of animals, is beyond the scope of this paper. It may, however, be mentioned that the formation of such excrescences is, to a certain degree, dependent on the food (**52**). This difference of the calcium-metabolism, and thus of the egg-shell, brings it about that the soft eggs of the Amphibia are not only more exposed to attacks of all sorts of animals, but that they must also be reared in comparatively damp places. Contrary to this the Sauropsidian eggs endure, even when their shell is thin, a much greater dryness. In certain respects the shell of a reptilian egg can thus be compared to the shell of a snail, for it is a well-known fact that the snails inhabiting dry countries have comparatively thicker shells than their relatives living in moister countries. Here it is enough to mention *Helix pomatia*, *H. pisana*, *H. niciensis*. Other examples and the literature referring to the subject have been quoted by Hesse (**44**).

Perhaps even the thickness of the shell of the eggs of birds will turn out to be in correlation with the amount of desiccation to which the eggs are exposed. As a rule, the egg-shell is abnormally thick only in the eggs of birds that have an open nest in warm or relatively warm countries, with more or less rain, less during the breeding season (*Struthio*, *Numida*, *Caccabis rufa*, *Francolinus grantii*, *Gypaëtus*, *Vultur*, *Pterocles*), also in some birds that build exposed nests on the tops of trees or on rocks (*Crax*, *Ardea*, *Gyps*) or in flat tracts of relatively dry countries (*Otis*), or that place their nests at least in drier places than their near relatives (*Grus*).

Thin or even very thin egg-shells are found in all birds that place their eggs under mounds of rotting vegetation (all *Megapodii*), in some that place them in burrows (*Puffinus*, *Galbula*, *Riparia*, *Trachyphonus*) or in hollow trees (*Rhamphestes*, *Monasa*, *Chelidoptera*, *Bucephala clangula*, *Pteroglossus*, *Jynx*, *Sturnus*, *Falco naumanni*). *Chelidon* and *Hirundo*, that have well closed nests of mud, lay likewise very thin-shelled eggs, and the same holds good for *Phylloscopus*, *Anthoscopus*, and *Textor*, that all build well-closed nests. The Eagle *Circaëtus*, that has likewise thin-shelled eggs, covers these, when leaving the nest, with green twigs, and although other Eagles do the same and have normally thick egg-shells, nevertheless *Circaëtus* may be referred to, for the egg-shell of none of these eagles is abnormally thick. Some birds building their nests in cool damp countries also have very thin egg-shells (*Branta*, *Eudromas*), and the same is true for some birds that lay their eggs on moist meadows (*Nyctea*, *Recurvirostra*, *Himantopus*, *Pelidna*), in the sand on the border of a river (*Ægialitis*) or other damp places (*Locustela*), or breed during the spring-rains (*Tetrao*). Thin egg-shells are also met with in birds that breed close to the ground or even among dense reeds (*Ardeola*, *Botaurus*), while their relatives breed on trees. *Fulica*, that frequently builds a floating nest, has likewise thin-shelled eggs, and so has also *Hydrochelidon*.

The difference of the thickness of the egg-shell becomes especially striking when the Vultures are compared with the Eagles, the Megapodii with the majority of the Galli, *Francolinus granti* with *Francolinus johnstoni*, *Numida* with *Colinus*, *Grus* with *Fulica*, *Ardea* with *Botaurus*, *Chetusia* with *Vanellus*, *Bucephala clangula* with *Bucephala islandica*, and *Falco naumanni* with the rest of the Falconidæ.

In spite of this, one must not forget that exceptions also exist. Even if one tries to explain the thin egg-shell of *Columba palumbus* by the observation that many Columbidæ breed in hollow trees or rock-fissures, and assumes that the Bucerotidæ originated, as indicated by *Aceros*, from birds having originally very thick egg-shells that became reduced to the normal thickness by the curious nesting habits of these birds, and even if one assumes also that a reduction of the egg-shell is going on in all those birds which the egg-shell shows over the cover of crystallised lime another one of fine granular lime* (*Podiceps*, *Sula*, *Phalacrocorax*, *Plotus*,

* This statement is based on the microscopical investigation of a transverse section of an egg-shell of *Phalacrocorax* kindly handed to me by Dr. E. Korb in Vienna.

Pelecanus, *Phœnicopterus*), ev[illegible] *Curs[illegible]ius* are just as difficult to explain as the a[illegible] *a arctica*, *Mergus cucullatus*, *Colymbus*, *Gallinula*, *Picumnus innominatus*, some species of *Larus* and of *Plautus* (10). All this shows that, before drawing a definite conclusion, the question needs further study, and all the more so since in this question also the size and the number of the pores of the egg-shells ought to be considered (95), but, as such a detailed investigation is beyond the limit of this paper, at present these tentative indications may be considered as sufficient.

The means to which the highly terrestrial Frogs have resorted to overcome the difficulty of rearing their offspring in dry places is well known, and has well been summarised by Hilzheimer (45).

In a previous paper (83) it has been pointed out that the fostering of the offspring observable in Mammals and Birds, and the epidermal coating of these animals, indicate that the foundation of their development was laid by the great climatic change at the end of the Carboniferous. Moreover, it was surmised that during the warm, almost tropical, Mesozoic time these animals inhabited the cooler mountain regions, for in the hot lowlands they were not capable of competing with the dominant Archosaurian Reptiles.

Something analogous seems to have happened with the Stegocephalia, for the foregoing considerations make it probable that the extinction of the Stegocephalia and the restriction of the Amphibia to damp regions, as well as the rise of the Reptiles, were also due to a climatic change. This change was evidently the strong Permo-Triassic desiccation. In this connection it is important to remark that during the change itself in the Upper Permian not typical Sauropsidians like Archosauria, but Pareiasauria and Theromorpha lived; thus Reptiles flourished that come, by their whole structure, nearer to the Amphibia and Mammalia than to the Sauropsida. The typical Archosaurians developed only in a very dry climate, and as proof one can mention the light structure of their bones, their bipedalism, that can only have developed in an open country, the exceptional thickness of the egg-shell of those bare-skinned types that became during the Mesozoic the ruling race [Dinosaurs (96)], and the fact that the remains of their primitive members are met with in greater number only in deposits of very dry character, as in the red Keuper marls of Würtemberg and the Cave Sandstone of South Africa.

These primitive Archosaurians are all carnivorous. Incidentally it may be remarked that light limb-bones, a high metabolism, and a great demand for albumen (carnivorous, cursorial type of animal) are all signs of hyperthyroidism, and that, on the other hand, a food very rich in albumen, or consisting exclusively of such, tends to augment, in dogs, the function of the thyroid gland (111). In birds a feeding with meat produces in analogous manner a hyperplasy of the thyroid gland, and the thyroid gland of the Malays in Java, that live chiefly on rice, is smaller than that of Europeans (5). All these changes are therefore important, for a carnivorous adaptation may quite well set in, when during the desiccation of some region its vegetation begins to become scarce. Of course, it is not meant hereby to explain *all* evolution by the coincidence of such changes; they are, however, mentioned to show what has to be considered when studying evolution. The importance of such considerations has lately again been emphasised by Hammett (36), and before this by Sir A. Keith (56).

Naturally it would have been quite impossible to write a paper dealing with such various questions as the foregoing one, without help from different sides. Apart from the gentlemen mentioned in the text, the well-known neurologist Prof. Baron C. Economo was so kind to call my attention to the work of Kraepelin, and the ornithologist Dr. O. Reiser helped me when studying the eggs of birds, Professors Dr. J. Bauer and Dr. C. Stejskal, both in Vienna, likewise helped me in my work. Sir Arthur Smith Woodward was so kind as to revise the English text. It affords me special pleasure to thank all these gentlemen for their help.

Literature.

(Regarding the Anatomy of Fossil Reptiles only these papers are quoted that contain typical figures.)

1. Andrews, C. W. On the Structure of the Skull in *Peloneustes philarchus*. Ann. Mag. Nat. Hist. (ser. 6) vol. xvi. London, 1895.—Williston, S. W. North American Plesiosaurs. Field Columbian Museum; Geolog. Ser. vol. ii. Chicago, 1903 (*Dolichorhynchops*).—*Idem.* The Temporal Arches of Reptilia. Biological Bulletin 1904 (*Cimoliosaurus*).—Huene, Fr. von. Ein neuer Plesiosaurier aus dem oberen Lias Württembergs. Jahreshefte d. Verein f. vaterländ. Naturkunde Württembergs, vol. lxxix. Stuttgart, 1923 (*Plesiosaurus*).
2. Ascher, L. Die Beziehungen der Schilddrüse zu Funktionsgebieten anderer Organe. Schweizer. medicin. Wochenschr. vol. viii. Basel, 1927.
3. Bauer, J. Innere Sekretion, ihre Physiologie, Pathologie und Klinik. (pp. 35–40). Berlin, 1927.
4. ——— *Ibid.* p. 271.
5. ——— *Ibid.* pp. 271 and 466.
6. Baumeister. Beitrag zur Anatomie der Rhinophiden. Zool. Jahrbüch. (Anatom. Abteil.) vol. xxvi. Jena, 1909.
7. Boas, J. E. V. Die Schläfenüberdachung und das Palatoquadratum. Morpholog. Jahrbuch, vol. xlix.—Bolkay, St. J. Elements of the Comparative Osteology of the Tailless Batrachians. Glasnika zemaljskog muzeja Bosni i Hercegovini, vol. xxxi. Sarajevo, 1919.
8. Bolkay, St. J. Die Schädel der Salamandrinen mit besonderer Rücksicht auf ihre systematische Bedeutung. Zeitschr. f. Anatom. u. Entwicklungsgesch. vol. lxxxvi. Berlin, 1928.
9. Boulenger, G. A. Catalogue of Chelonians, Rhynchocephalians, and Crocodiles of the British Museum. London, 1889.
10. Data compiled from: Brehm, Tierleben (4th edit.) Vögel bearbeitet v. O. Zur Strassen. Leipzig, 1913.—Nehrkorn, A. Katalog der Eiersammlung nebst einer Beschreibung der aussereuropäischen Eier (2 edit.). Leipzig, 1910.—Hartert, E. Die Vögel der palaarktischen Fauna, vols. i.–iii. Berlin, 1912–22.
11. Broili, F. Unpaare Elemente in Schädel der Tetrapoden. Anatom. Anzeiger, vol. xlix. Jena, 1917.
12. Broili, Fr. Beobachtungen an *Cochleosaurus bohemicus*. Palæontographica, vol. iii. Stuttgart, 1905.
13. Broom, R. A Comparison of the Permian Reptiles of North America with those of South Africa. Bull. Amer. Mus. Nat. Hist. vol. xxviii. New York, 1910.—Pearson, H. S. The Skull of the Dicynodont Reptile *Kannemeyeria*. Proc. Zool. Soc. London, 1924.
14. ——— Studies on the Permian Temnospondylous Stegocephalians of North America. Bull. Amer. Mus. Nat. Hist. vol. xxxii. New York, 1913.
15. Brugsch. Innere Sekretion. In: Kraus and Brugsch, Spezielle Pathologie und Therapie innerer Krankheiten, vol. i. Berlin, 1919.
16. Case, E. C. Description of a Skeleton of *Dimetrodon incisivus* Cope. Bull. Amer. Mus. Nat. Hist. vol. xxviii. New York, 1910.
17. ——— A Revision of the *Cotylosauria* of North America. Carneg. Inst. Washington, Publication No. 145. Washington, 1911.
18. ——— The Permocarboniferous Red Beds of North America and their fauna. Carneg. Inst. Washington, Publication No. 207. Washington, 1915.—Williston, S. W. Restorations of some American Permocarboniferous Amphibians and Reptiles. Journal of Geology. Chicago, 1914.
19. ——— Environment of Tetrapod Life in the Later Palæozoic of Regions other than North America. Carneg. Inst. Washington, Publication No. 375. Washington, 1926. – Moodie, R. L. The Coal Measures Amphibia of North America. Carneg. Inst. Washington, Publication No. 238. Washington, 1916.—Romer, A. S. The Pennsylvanian Tetrapods of Linton. Bull. Amer. Mus. Nat. Hist. vol. lix. New York, 1930.
20. Coe & Kunkel. Studies of the Californian Limbless Lizard *Anniella*. Trans. Connect. Acad. of Science, vol. xii. Cambridge, 1907.

21. Credner, H. Die Stegocephalen und Saurier aus dem Rothliegenden, Teil IV. Zeitschr. d. deutsch. geolog. Gesellsch. Berlin, 1883.—Broili, Fr. Ueber die Hautbedeckung der Archægosauridæ und Actinodontidæ. Zeitschr. d. deutsch. geolog. Gesellsch. vol. lxxix. Berlin, 1928.

22. Delcourt-Bernard, & Mayer. Recherches sur le métabolisme de base. Annales de Physiolog. et de Physiochim. biolog. Tome i. Paris, 1925.

23. D'Erasmo, G. La fauna e l'etá dei calcari a ittioliti di Pietraroia. Palæontograf. Italica, vol. xxi. Pisa, 1915.

24. Dieterle, H. Die Athyreosis. Virchow's Archiv f. Pathologie, vol. clxxxiv. Berlin, 1906.—Landauer, W. Thyrogenous Dwarfism in the Domestic Fowl. Amer. Journ. of Anatomy, vol. xliii. Philadelphia, 1929.

25. Dollo, L. Note sur le Batracien de Bernissart. Bull. Mus. Roy. Hist. Nat. Belg. vol. iii. Bruxelles, 1884.

26. Douthitt, H. Structure and Relationships of *Diplocaulus*. Contrib. to Walker Museum. Chicago, 1917.

27. Dezewicki, S. Ueber den Einfluss, der Schilddrüsenextirpation bei der Zauneidechse. Archiv f. Entwicklungsmechanik, vol. cxiv. Berlin, 1929.

28. Fraas, E. Die Ichthyosaurier der Süddeutschen Trias und Jura-Ablagerungen. Tübingen, 1891.

29. Fries, C. Zur Phylogenie des Schildkrötenpanzers. Zoologischer Anzeiger, vol. lxi. Leipzig, 1924.

30. Fritsch, A. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Prag, 1883–1902.

31. Fröböse, H. Anatomie des Legedarmes und Kalkschalenbildung beim Huhn. Zeitschr. mikroskop. u. anatom. Forschung, vol. xiv. Leipzig, 1928.

32. Gervais, P. Recherches sur l'ostéologie de plusieures espèces d'Amphisbènes. Annales Sciences Naturelles (Zool.), vol. xix. Paris, 1853.

33. Gilmore, Ch. W. On *Troödon validus*. University of Alberta, Department of Geology. Edmonton, 1924. – Sternberg, C. M. A New Armoured Dinosaur from the Edmonton Formation of Aberta. Trans. Roy. Soc. Canad. vol. xxii. Ottawa, 1928.

34. ——— A Mounted Specimen of *Dimetrodon gigas*. Proc. U.S. National Mus. Washington, 1919.

35. Haas, G. Ueber die Kaumuskulatur und die Schädelmechanik einiger Wühlschlangen. Zoolog. Jahrbücher, Abt. f. Anatom. u. Ontogen, vol. lii. Jena, 1930.

36. Hammett, F. S. Thyroid and Differential Development. Endokrinologie, vol. v. (Festschrift für Biedl). Leipzig, 1929.

37. Harpuder, —. Ueber die Permeabilität der Haut und ihre Beziehung zur Bäderwirkung. Zeitschr. f. wissenschaftl. Bäderkunde, vol. iv. Berlin, 1929.

38. Haughton, S. H. Investigations in S. African Fossil Reptiles and Amphibia.—Part 13. Annals South African Mus. vol. xxii. Cape Town, 1925.

39. ——— *Ibid.* Part 1. Annals South African Mus. vol. xii. Cape Town, 1915.

40. ——— A Bibliographic List of Pre-Stormberg Karroo Reptilia, with a Table of Horizons. Transact. Roy. Soc. S. Africa, vol. xii. Cape Town, 1925.

41. ——— A Review of the Reptilian Fauna of the Karroo. Trans. Geolog. Soc. South Africa, vol. xxii. Cape Town, 1919.

42. Heinroth, O. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht, und Brutdauer. Journal für Ornithologie. Berlin, 1922.

43. Hesse, R. Tiergeographie auf ökologischer Grundlage, p. 168. Jena, 1924.

44. ——— *Ibid.* (p. 424).

45. Hilzheimer, M. Handbuch der Biologie der Wirbeltiere, pp. 217–225. Stuttgart, 1913.

46. Hintsche, E. Untersuchungen an Stützgeweben.—II. Ueber Knochenbildungsfactoren. Zeitschr. f. mikroskop. u. Anatom. Forschung, vol. xiv. Leipzig, 1928.—Müller, W. Die normale und pathologische Physiologie des Knochens. Leipzig, 1924. Literature on the subject in Hintzsche, E. Die Osteoblastenlehre und die neueren Anschauungen vom normalen Verknöcherungsvorgang. Ergebnisse d. Anatom. u. Entwicklungsgesch, vol. xxvii. Berlin, 1927.

47. Hoffker, J. *Archegosaurus decheni* Goldfuss. Untersuchung des Schädelbaues. Palæontologia Hungarica, vol. i. Budapest, 1927.

48. Hooley, R. W. The Skeleton of *Ornithodesmus latidens*. Quart. Journ. Geol. Soc. vol. lxix. London, 1913.—Eaton, G. F. Osteology of *Pteranodon*. Memoirs Connecticut Acad. Arts and Science, vol. ii. 1910.

49. Huene, Fr. von. The Skull-elements of the Permian Tetrapoda. Bull. Amer. Mus. Nat. Hist. vol. xxxii. New York, 1913.

50. ——— Neubeschreibung des permischen Stegocephalen *Dasyceps bucklandi*. Geolog. u. Palæontolog. Abhandlungen, vol. xii. Jena, 1910.

51. ——— Die Südafrikanische Karroo-Formation als geologisches und faunistisches Lebensbild, in "Fortschritte der Geologie u. Palæontologie," Heft 12. Berlin, 1925.

52. Huxley, J. S. The Annual Increment of the Antlers in the Red Deer. Proc. Zool. Soc. London, 1926.

53. Jaekel, O. *Gephyrostegus bohemicus*. Zeitschrift. deutsch. Geolog. Gesell. vol. liv. Berlin, 1902.

54. ——— Ueber die Klassen der Tetrapoden. Zoolog. Anzeiger, vol. xxxiv. 1909.

55. ——— Ueber Keraterpeton, Diceratosaurus, und Diplocaulus. Neues Jahrb. f. Min. Geol. u. Palæont. Stuttgart, 1903.

56. Keith, Sir A. The Evolution of Human Races in the Light of the Hormone Theory. Bullet. Johns Hopkins Hospital, vol. xxxiii. Baltimore, 1922.

57. Kellog, R. G. The History of Whales. The Quart. Rev. of Biology, vol. iii. Baltimore, 1928.

58. König, — . Chemie der menschlichen Nahrungs- und Genussmittel. Nachtrag zu Band I. (pp. 570). Berlin, 1919.

59. Kraepelin, E. Psychiatrie, ein Lehrbuch für Studierende und Ärtzte, vol. i. Leipzig, 1903.

60. Landauer, W. Thyrogenous Dwarfism in the Domestic Fowl. Amer. Journ. of Anatom. vol. xliii. Philadelphia, 1929.—Falta, W. Erkrankungen der Blutdrüsen in Mohr & Staelin, Handbuch der inneren Medicin, vol. iv. Teil 2. Berlin, 1927.

61 Mark, R. E. Untersuchungen über den Einfluss verschiedener Höhenlagen auf die Schilddrüse bei Hunden. Archiv f. experimentelle Patholog. u. Pharmakolog. vol. cxxxix. Leipzig, 1929.

62. Meyer, H. von. Salamandrinen aus der Braunkohle am Rhein und in Böhmen. Palæontographica, vol. vii. Cassel, 1859-61.

63. Moodie, R. L. An American Jurassic Frog. Amer. Journ. of Science, (ser. 4) vol. xxxiv. New Haven, 1912.

64. ——— The Ancestry of the Caudate Amphibia. American Naturalist, vol. xlii. 1908.

65. Mook, Ch. C. Individual and Age Variation in the Skull of recent Crocodilia. Bull. Amer. Mus. Nat. Hist. vol. xliv. New York, 1921.

66. Murayamo, Terukuni. Ueber die Balanzierstange bei Hynobiuslarven. Folia anatomica Japonica, vol. vi. Tokye, 1928.

68. Nicholas. A Balancer in the Larvæ of *Ambylstoma*. American Naturalist, vol. lix. New York, 1925.

69. Nick, L. Das Kopfskelet von *Dermochelys coriacea*. Zoolog. Jahrbücher, vol. xxxiii. Jena, 1912.—Völker, H. Das Stamm Gliedmassen und Hautskelett von *Dermochelys coriacea*. Zoolog. Jahrbucher, vol. xxxiii. Jena, 1913.

70. Nikitin, B. Some Peculiarities in the Development of the Vascular System in *Xenopus* Bullet. Soc. Naturalistes, vol. xxxiv. Moscou, 1925.

71. Noble, G. K. The Phylogeny of the Salientia. Bull. Amer. Mus. Nat. Hist. vol. xlvi. New York, 1922.—*Idem*. An Outline of the Relation of Ontogeny to Phylogeny within the Amphibia. American Museum Novitates, 1925.—*Idem*. The Value of Life-history Data in the Study of the Evolution of the Amphibia. Annals New York Acad. of Sciences, vol. xxx. New York, 1927.—Bolkay, St. J. Die Schädel der Salamandrinen mit besonderer Berücksichtigung ihrer systematischen Bedeutung. Zeitschr. f. Anatom. u. Entwicklungsgeschichte, vol. lxxxvi. Berlin, 1928.

72. ——— A New Spadefoot Toad from the Oligocene of Mongolia. Amer. Museum Novitates. New York, 1924.

73. ——— Two New Fossil Amphibia of Zoogeographic Importance from the Miocene of Europe. Amer. Museum Novitates. New York, 1928.

74. ——— Further Observations on the Life-history of the Newt, *Triturus*. Amer. Museum Novitates. New York, 1919.

75. ——— The Value of Life-history Data in the Study of the Evolution of Amphibia. Annals New York Acad. of Sciences, vol. xxx. New York, 1927.

76. Nopcsa, Fr. Kallokibotium, a Primitive Amphichelydean Tortoise from the uppermost Cretaceous of Hungary. Palæontolog. Hungarica, vol. i. Budapest, 1923.

77. Nopcsa, Fr. Notizen über Dinosaurier, 2 Teil: die Riesenformen unter den Dinosauriern. Centralbl. f. Min. Geol. & Palæont. Stuttgart, 1917.

78. ——— Vorläufige Notiz über die Pachyostose und Osteosklerose mariner Wirbeltiere. Anatom. Anzeiger, vol. lvi. Jena, 1923.

79. ——— Festrede gehalten von ... anlasslich des Besuches der Palæontolog. Gesellschaft im M. Kir. Földtani Intézet. Budapest, 1928.

80. ——— Reversible and Irreversible Evolution. Proc. Zool. Soc. London, 1923.

81. ——— Ueber prozœle und opistozœle Wirbel. Anatom. Anzeiger. vol. lxix. Jena, 1930.—*Idem.* Ueber die Orientierung konvexokonkaver Gelenkflächer. Anatom. Anzeiger, vol. xlvi. Jena, 1930 (in print).

82. ——— Palæontological Notes on Reptiles. Geologica Hungarica, Ser. Palæontologica. Budapest, 1928.

83. ——— Noch einmal Proavis. Anatom. Anzeiger, vol. lxvii. Jena, 1929.

84. Parks, W. A. *Struthiomimus samueli.* Univers. of Toronto Studies, Geolog. Series. Toronto, 1920.

85. ——— *Arrhinoceratops brachyops*, a new Genus and Species of Ceratopsians. Univ. of Toronto Studies, Geolog. Series, No. 19. Toronto, 1925.

86. Peter, K. Zur Anatomie eines ostafrikanischen Apoden. Zoolog. Jahrbücher (Abt. f. Anatom. u. Ontogenie), vol. xxvi. Jena, 1908.

87. Peyer, B. Die Entwicklung des Schädelskelettes von *Vipera aspis*. Gegenbaur Morpholog. Jahrbuch, vol. xliv. Leipzig, 1912.

88. Romer, A. S. The Pennsylvanian Tetrapods of Linton. Bull. Amer. Mus. Nat. Hist. vol. lix. New York, 1930.

89. Sampelayo, P. H., & Cincunegui, M. Fauna de la Cuenca de Ribesalbos in Cuenca de esquistos bituminosos de Riebesalbes. Boletin Institut. Geolog. de España, vol. vi. (ser. 3). Madrid, 1926.

90. Sarasin, P. & F. Zur Entwicklungegeschichte und Anatomie der Ceylonesischen Blindwühle *Ichthyophis glutinosus.*

91. Schmidt, W. J. Die Kalkschale des Sauropsideneies als geformtes Sekret. Zeitschr. f. Morpholog. u. Oekologie der Tiere, vol. xiv. Berlin, 1929.

92. Sollas, W. J. On the Structure of *Lysorophus* as exposed by serial Sections. Phil. Trans. Roy. Soc. vol. ccix. London, 1920.

93. Stremme, H. Ueber die durch Bandverknöcherung hervorgerufene proximale Verschmelzung der Mittelhand- oder Mittelfussknochen eines Reptils. Archiv f. Biontologie, vol. iv. Berlin, 1920.

94. Stromer, E. Fr. Ergebnisse der Forschungsreisen Prof. Stromers in den Wüsten Egyptens, II. Wirbeltierreste der Baharije Stufe. Abhandl. Bayer. Akad. d. Wiss. München, 1915.—Nopcsa, Fr. Sexual Differences in Ornithopodous Dinosaurs. Palæobiologica, vol. ii. Wien, 1929.

95. Szielasko, A. Die Bedeutung der Eierschalenstructur für die Systematik. Journal f. Ornitholog. vol. lxi. Leipzig, 1913.

96. Straelen, V. van, & Denaeyer, M. E. Sur des œufs fossiles du Cretacé superieur de Rognac en Provence. Acad. Roy. Belg. Bullet. Classe des Sciences. Bruxelles, 1923.—Van Straelen, V. The Microstructure of the Dinosaurian Eggshells from the Cretaceous of Mongolia. American Museum Novitates, No. 173. New York, 1925.

97. Versluys, J. Das Streptostylie-Problem. Zoolog. Jahrbücher Suppl., Band xv. Jena, 1912.

98. ——— Die Salamander und die ursprünglicher vierbeinigen Landwirbeltiere. Naturwiss. Wochenschr. vol. viii. Berlin, 1909.

99. Vidal, L. M. Nota geologica y paleontologica sobre el Jurasico superior de la provincia de Lérida. Bolet. Instit. Geologico España, vol. xxxvi. Madrid, 1915.—Fejérváry, G. J. Kritische Bemerkungen zu Osteologie, Phylogenie und Systematik der Anuren. Archiv für Naturgeschichte, vol. lxxxvii. (Abt. A). Berlin, 1921.

100. Vogt. Innere Sekretion und Balneologie. Zeitschrift f. wissensch. Bäderkunde, vol. iii. Berlin, 1929.—*Idem.* Badewirkung und Hautfunktion. Zeitschrift f. wissensch. Bäderkunde, vol. iv. Berlin, 1930.

101. Wallis, K. Ueber den Knochenkallus beim Kaltblüter. Zeitschr. f. Zellforsch. u mikroskop. Anatom. vol. vii. Berlin, 1928.—Wurmbach, H. Histologische Untersuchungen über die Heilung von Knochenbrüchen bei Amphibien. Zeitschr. f. Wiss. Zoolog. vol. cxxix. Leipzig, 1927.—Fujinami & Akira. Ueber die Gewebsveränderungen bei der Heilung von Knochenfrakturen. Beiträge z. patholog. Anatom. u. allgem. Pathologie, vol. xxix. Jena, 1901.

102. WATSON, D. M. S. The Structure, Evolution, and Origin of the Amphibia: the orders Rachitomi and Stereospondyli. Phil. Trans. Roy. Soc. vol. ccix B. London, 1919.—*Idem.* The Carboniferous Amphibia of Scotland. Palæontologia Hungarica, vol. i. Budapest, 1926.—*Idem.* The Evolution and Origin of the Amphibia. Phil. Trans. Roy. Soc. vol. ccxiv B. London, 1928.

103. ——— The Structure, Evolution, and Origin of the Amphibia: the orders Rachitomi and Stereospondyli. Phil. Trans. Roy. Soc. vol. ccix B. London, 1919.

104. ——— The Evolution and Origin of the Amphibia. Phil. Trans. Roy. Soc. vol. ccxiv B. London, 1926.

105. ——— On the Skull of a Pareiasaurian Reptile. Proc. Zool. Soc. London, 1914.

106. ——— The Deinocephalia, an order of Mammal-like Reptiles. Proc. Zool. Soc. London, 1914.

107. ——— *Microphlis stowi*, a Temnospondylous Amphibian from S. Africa. Geological Magazine (dec. 5), vol. x. London, 1913.

108. ——— The Carboniferous Amphibia of Scotland. Palæontologia Hungarica, vol. i. Budapest, 1923.

109. ——— *Batrachiderpeton lineatum.* Proc. Zool. Soc. London, 1913.

110. ——— *Batrachiderpeton lineatum.* Proc. Zool. Soc. London, 1913.

111. WEGELIN, C. Die Schilddrüse, in Handbuch der speciellen pathologischen Anatomie und Histologie. Drüsen mit innerer Sekretion. Berlin, 1921.

112. WIEDERSHEIM, R. Das Kopfskelett der Urodelen. Morpholog. Jahrbuch, vol. iii. Leipzig, 1899.

113. WILLISTON, S. W. New or little known Permian Vertebrates, *Trematops*, new Genus. Journal of Geology, vol. xvii. Philadelphia, 1909.- MEHL, M. *Trematops thomasi*, a new Amphibian. Journal of Geology, vol. xxxiv. Chicago, 1926.

114. ——— Synopsis of the American Permocarboniferous Tetrapoda. Contribution to Walker Museum. Chicago, 1916.

115. ——— American Permian Vertebrates. Chicago, 1911.

116. WIMAN, C. Die Kreide-Dinosaurier aus Shantung. Palæontolog. Sinica (ser. c.), vol. vi. Peking, 1929.—GILMORE, CH. W. A nearly complete articulated skeleton of *Camarasaurus*. Memoirs Carnegie Museum, vol. x. Pittsburgh, 1925.—HOLLAND, W. J. The Skull of *Diplodocus*. Memoirs Carnegie Museum, vol. i. Pittsburgh, 1924.

117. ——— Ueber die Stegocephalen *Tertrema* und *Lonchorhynchus*. Bull. Geol. Institut. of Upsala, vol. xiv. Upsala, 1917.

118. WODZICKI, K. La vascularisation des appendices cutanés chez les Oiseaux. Bull. Acad. Polon. Sciences et Lettres. Cracovie. 1929.- CLARA, M. Die arterio-venösen Anastomosen der Vögel und Saugetiere. Ergebnisse d. Anatom. u Entwicklungsgesch. vol. xxvii. Berlin, 1927.

119. WURMBACH, H. Histologische Untersuchungen über die Heilung von Knochenbrüchen bei Amphibien. Zeitschr. Wiss. Zoolog. vol. cxxix. Leipzig, 1927.—*Idem.* Biologische Untersuchungen über die Heilung von Knochenbrüchen. Zeitschr. f. Wiss. Zoolog. vol. cxxxii. Leipzig, 1928.- WALLIS, K. Ueber den Knochenkallus beim Kaltblüter. Zeitschr. f. Zellforsch. u. mikroskop. Anatom. vol. vii. Berlin, 1928.

120. ——— Histologische Untersuchungen über die Heilung von Knochenbrüchen bei Amphibien. Zeitschr. f. Wiss. Zoolog. vol. cxxix. Leipzig, 1927.- WALLIS, K. Ueber den Knochenkallus beim Kaltblüter. Zeitschr. f. Zellforsch. u. mikroskop. Anatom. vol. vii. Berlin, 1928.

47. The proportions of Birds' Wings and their Changes during Development.

By B. J. MARPLES, B.A., the Victoria University of Manchester*.

[Received May 10, 1930: Read November 4, 1930.]

(Text-figures 1–7.)

I. INTRODUCTION.

The proportions of the various parts of birds' wings vary very much from one species to another, and in those species which have been investigated there are also great changes in the proportions during development. Beebe and Hartley (1916), working in British Guiana, investigated the changes in the proportions of the wing during development in some ten species of birds, and published graphs of these. The only other work of a similar nature of which I am aware is that of T. J. Parker (1891), who gave graphs of the changes in proportion of various parts of the skeleton, including the wing, of *Apteryx*. Latimer (1927) did similar work on the skeleton of the fowl, only much more fully, but in both these cases it is the changes in proportion of the wing to the rest of the body which are considered.

As it seemed desirable that Beebe's method should be applied to a larger number of birds, the present investigation was undertaken, and this paper deals with the wings of ten species of British birds. It is hoped that when a series of allied forms has been obtained some light may be thrown upon the significance of these changes in proportion, and also, possibly, on the phylogenetic relationships of the various species.

In addition to the work on the different stages in development of these ten species, the wings of the adults of as many species of birds as possible have been measured. There is a great difference in the proportions of the wing amongst birds, and though in some cases it appears to be correlated with the mode of flight, in others no such correlation is apparent, and it is hoped that a large series of measurements will help towards the solution of the problem.

The investigation is therefore a study of the proportions of birds' wings and the changes in proportion which take place during development, with the object of discovering their significance and possible bearing on the phylogenetic history of the species.

II. MATERIAL AND METHODS.

The changes in proportion of the wing during development have been studied in the following ten species of birds:—The Common Tern, *Sterna fluviatilis*; the Arctic Tern, *Sterna macrura*; the Sandwich Tern, *Sterna cantiaca*; the Lesser Tern, *Sterna minuta*; the Black-headed Gull, *Larus ridibundus*; the Ringed Plover, *Ægialitis hiaticola*; the Eider Duck, *Somateria mollissima*; the Budgerigar, *Melopsittacus undulatus*; the Blackbird, *Turdus merula*; the Song-Thrush, *Turdus musicus*. For the sake of uniformity all the specific names used in this paper are those given by Evans (1898).

The Thrush and Blackbird material was obtained from nests kept under observation during laying and incubation, and in these cases the age is known; but in the other species nothing is known of the ages either of the embryos or of the young birds. The young birds used were picked up dead in the nesting colony, where they are usually fairly plentiful. The adult measurements of the Sandwich and Lesser Terns were taken from skeletons in the Natural History Museum,

* Communicated by Prof. J. S. DUNKERLY, D.Sc., Ph.D., F.Z.S.

South Kensington, and so come from localities entirely different from those of the earlier stages. The Budgerigars were of the ordinary wild green form such as are commonly kept in aviaries. They were bred in captivity, but as their power of flight appears to be perfectly normal, and is constantly exercised, there seems to be no objection to using them for this purpose. They lived in a large out-door aviary all the year round and bred freely.

No attempt at all was made to use statistical methods. It would be extremely hard to obtain large numbers of embryos and young at definite stages in development, and for the present purpose great accuracy is not necessary, as the changes considered are relatively large. The measurements each represent a single individual, and the fact that the points fall upon a reasonably smooth curve makes it probable that individual variations are small, and may be neglected in this particular work.

The three main parts of the wing:—humerus, ulna, and manus were measured. The two parts of the manus, metacarpal and digit, were also measured, but they are not considered in the present paper. The method employed for the earlier embryos was to stain by the Victoria Blue method and mount as microscopical preparations, by which technique only the cartilage is stained, rendering the skeleton of the wing very clearly visible. The various parts were measured by means of a microscope with a mechanical stage having a vernier scale attached. The wings of the larger embryos and smaller nestlings, in which ossification had proceeded too far for the above method to be used, were merely dehydrated and cleared in xylol, when the bones became clearly visible. Any shrinkage produced by the clearing and mounting processes is of no importance, since it is the relative, and not the absolute, lengths which are required. For reasons previously stated it was considered sufficiently accurate to measure the wings of the larger stages by means of needle-pointed callipers and a millimetre scale.

In this way the length of the wing and of its component parts at various stages in development were obtained. From these data the lengths which the parts would have if the wing at that stage was magnified until it was the same length as that of the adult were calculated. This was done by multiplying the actual length of the part by the fraction L/l, where L is the total length of the adult wing and l the length of the wing at the particular stage. When this has been done, the sum of the calculated lengths of the parts of each wing is equal to the total length of the adult wing. This method appears to have been the one used by Beebe and Hartley, but in the figures published by them the sum of the lengths of the parts is not always constant.

Graphs were plotted, using these figures, to show the change in proportion of the wing during development. It was found best to use the adult wing as a constant as, if some other part of the body, such as the length of the vertebral column, is used, the changes in proportion of the whole wing to this other part tend to obscure the changes in proportion between the parts of the wing itself. Time is plotted along the abscissa and calculated length up the ordinate, the time of hatching being indicated by a vertical dotted line. The individuals were arranged in order and spaced out along the abscissa according to their estimated ages. In this way it is hoped to get approximately the true shape of the curve, and so to be able to draw conclusions as to the rate at which the changes take place, but it must be remembered that the ages are only estimated from the comparison of the series of specimens, and are not to be relied upon. In describing the young, the terms "nestling" and "fledgling" are used for convenience to denote early and late young ones, though of the species considered only the Blackbird, Thrush, and Budgerigar have true nestlings, the others having active downy young.

In investigating the proportions of the wing of adult birds similar methods were employed. Again no attempt at statistical treatment was made, and the measurements are of single individuals, and not the average of a large number. In a few instances several individuals of the same species were measured, and the

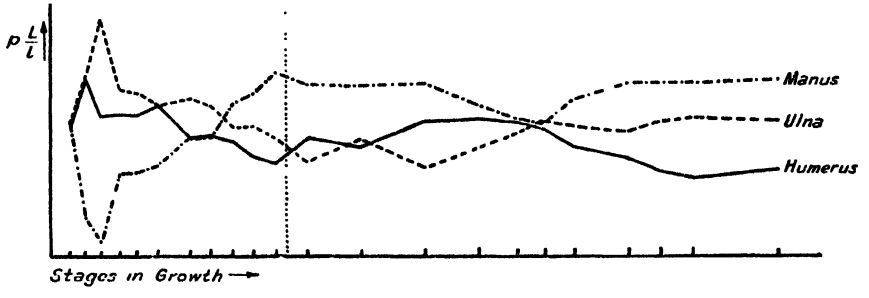
lengths were found to vary very little. All measurements were made using needle-pointed callipers and a millimetre scale, and all the bones of the wing except the radius were measured. For the sake of uniformity the right wing was used whenever possible. The lengths of the bones were then expressed as percentages of the total wing-length, and these are the figures given in this paper—never the actual measurements. So far only about eighty species have been measured, belonging to many different orders. I am indebted to Prof. E. S. Goodrich for kind permission to measure the bird-skeletons in the University Museum and Department of Zoology at Oxford, and to Prof. J. S. Dunkerly for similar facilities at Manchester.

III. Description of Wing-developments.

1. *The Terns.*

The Common Tern, *S. fluviatilis*, was the species which was investigated most fully. Twenty-two stages were measured, and of these eleven were embryos. In the very earliest stage, when the skeleton of the wing can only just be made out, all three parts are equal in length, but soon a very abrupt change takes place, the ulna, and to a lesser extent the humerus, increasing rapidly, while the manus decreases, so that the parts come to differ in length more than they do at any other time during the whole development. A little later a sudden reversal takes place, and

Text-figure 1.



Wing-development of Common Tern.

The graphs in text-figs. 1–6 express the changes in length of the various parts of the wing relative to its total length. The values plotted as ordinates are not the actual measurements, but are calculated in the following manner:—The actual length of each part, p is multiplied by the fraction L/l, where L is the total length of the adult wing and l the total length of the wing at the particular stage. In this way only the changes in length of the parts relative to one another are shown, and not the change due to increase in size of the bird. The different parts are denoted as follows:—Humerus ————, Ulna - - - - -, Manus – • – • –, and the time of hatching is shown by the vertical dotted line

the manus increases steadily uptil the time of hatching, while the ulna and humerus decrease and become considerably shorter than the manus. Just after hatching, the ulna and humerus are about the same length, but later there is a divergence, the humerus increasing until the late nestling period, after which it decreases to its final length in the adult. In the late nestling period there is a time when all the parts of the wing have approximately the same length, and after this the manus increases, the humerus decreases, and the ulna remains the same.

In the Arctic Tern, *S. macrura*, ten stages were measured, and of these six were embryos. The wing-development is very like that of the Common Tern, as would

be expected, since the birds are so closely related. In the earliest stage obtained the ulna is very much the longest and the manus very much the shortest, as in the corresponding stage of the Common Tern, and the manus increases until hatching, while the ulna and humerus decrease. There is an increase in the humerus in the nestling period, but this seems to take place rather earlier than in the Common Tern. There does not seem to be a time when the parts are equal in length, but this is uncertain owing to the scarcity of late stages.

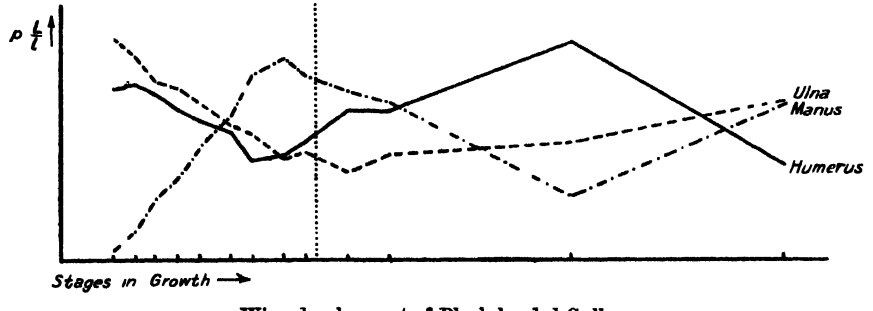
In the Sandwich Tern, *S. cantiaca*, six stages were measured, only one being an embryo, and that one on the point of hatching. Just before hatching, the manus is much the longest and the humerus much the shortest. Throughout the period covered the ulna increases gradually; the humerus increases till the nestling period, when it is the longest part, and then decreases to the adult, while at the same time opposite changes take place in the manus, which is the shortest part in the late nestling. These changes in the humerus and manus are an exaggeration of those found in the Common and Arctic Terns, in which the same increase and decrease take place, but the manus remains the longest part throughout.

Of the Lesser Tern, *S. minuta*, only five stages have been obtained, and so very little is known of its development. It appears to be of the same type as that of the other Terns. In the embryo the manus increases up to hatching, while the ulna and humerus decrease. As none of the stages is in the nestling period, it is not known whether the increase in the humerus takes place, but the change from the fledgling to the adult is the same as in the other species.

2. *The Black-headed Gull.*

Thirteen stages of the Black-headed Gull, *L. ridibundus*, were measured, but, as ten of these were embryos, the development during the later period is not known in detail. The development during the embryonic period is very similar to that of the Terns, and the changes are remarkably regular. In the earliest stage obtained

Text-figure 2.



Wing-development of Black-headed Gull.

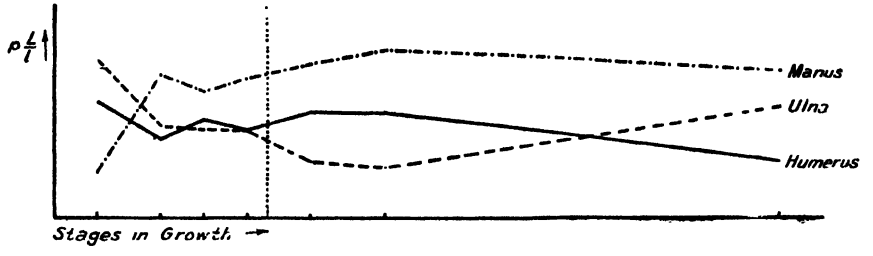
the manus is short and the humerus and ulna long, the ulna being the longest of the three. Until just before hatching there is a steady decrease in the humerus and ulna and an increase in the manus. From hatching to maturity the ulna increases slightly, but the humerus and manus change in opposite directions, so that in the fledgling the humerus is very long and the manus short. In the adult the humerus is the shortest segment, while the ulna and manus are about the same. This great increase of the humerus in the fledgling recalls that found in the Terns, only it is carried much further. In this respect the Common Tern, the Sandwich Tern, and the Black-headed Gull form a series. In the Common Tern the humerus

increases and the manus decreases, but the manus is always the longer. In the Sandwich Tern the same process takes place, but the humerus becomes longer than the manus, while in the Black-headed Gull the humerus becomes very much longer than the manus, so that the difference between them is about three times as much as it is in the Sandwich Tern. The total length of the adult wing is about the same in the Sandwich Tern and the Black-headed Gull. Altogether there is a great similarity between the wing-development of the Terns and the Black-headed Gull.

3. *The Ringed Plover.*

In the Ringed Plover, *Æ. hiaticola*, only seven stages were measured, four being embryos; none were fledglings. In the earliest the manus is the shortest and the ulna longest. The humerus decreases at first, but has a period of greater length in the late embryo. It increases again slightly in the nestling and finally decreases to the adult. The ulna decreases steadily during the embryonic and nestling

Text-figure 3.

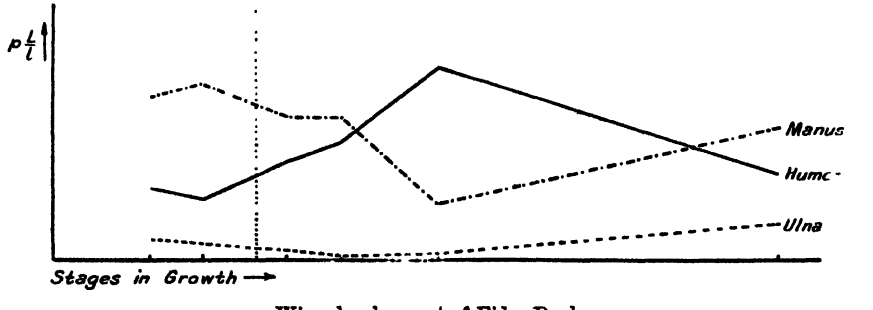


Wing-development of Ringed Plover

periods, after which it increases to the adult. The manus increases throughout the embryonic and nestling periods, and then increases to the adult.

The wing-development of this species, so far as it is known, is similar to that of the species already considered, but it is unfortunate that no fledgling stages were obtained. The same increase of the humerus in the nestling is seen, but there is no decrease in the manus as in the other forms, unless it takes place in the fledgling. The development of the wing during the embryonic period and the proportions of the wing in the earliest stage are very like those of the Terns.

Text-figure 4.



Wing-development of Eider Duck.

4. *The Eider Duck.*

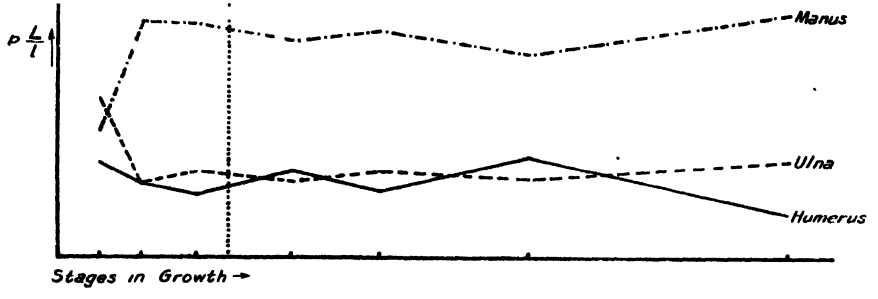
Six stages were measured of the Eider Duck, *S. mollissima*, two being late embryos and none fledglings. The most remarkable thing about the wing-develop-

ment of this species is the fact that the ulna remains practically constant and considerably shorter than the other segments from embryo to adult. The wing of the embryo has about the same proportions as that of the adult, the ulna being shortest, the manus longest, and the humerus about half way between. The humerus increases and the manus decreases, so that in the late nestling period their positions are reversed, and the humerus is much the longest segment. The changes of the humerus and manus in the Duck are similar to those in the Black-headed Gull so far as they are known, but the shortness of the ulna distinguishes the duck-wing from that of the Gull and from all the other species which have been investigated.

5. *The Budgerigar.*

Seven stages of the Budgerigar, *M. undulatus*, were measured, four being embryos, two nestlings, and one an early fledgling. Remarkable features are the great length of the manus and the constancy of all the parts from an early embryonic stage. In the first embryo, which is a very early one, the ulna is the longest, the humerus shortest, and the manus in between. From here the manus increases rapidly and then remains practically constant till the adult, while the ulna and

Text-figure 5.



Wing-development of Budgerigar.

humerus decrease and remain more or less constant and equal in length till the fledgling, after which they diverge slightly, the humerus decreasing

The adult Budgerigar is remarkable for the great length of the manus. Of all the adult wings measured it is only surpassed by the Swifts and Penguins, and it is interesting to find that the wing already has these unusual proportions in the early embryo. The same type of wing, with the long manus, is found in the Terns, but the development could hardly be more different.

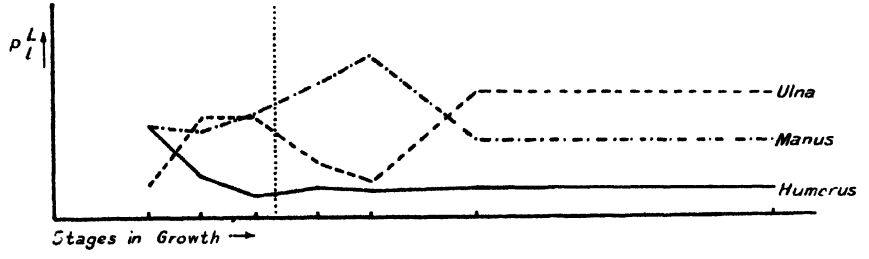
6. *The Blackbird.*

In the Blackbird, *T. merula*, six stages were measured, of which two were embryos. In the adult the ulna is much the longest segment, while the humerus and manus are about the same length, and the adult proportions are acquired about the time the young bird is ready to fly. In the earliest stage the manus is the longest and the humerus the shortest. The manus increases to the early nestling and then decreases rapidly to the fledgling. The ulna increases until just before hatching, decreases in the nestling, and then increases to its final length during the fledgling period. The humerus decreases during the embryonic and nestling periods, and then increases again till, in the fledgling, it is the same as the manus.

7. The Song-Thrush.

In the Song-Thrush, *T. musicus*, seven stages were measured, three being embryos and one about to fly. The development, as one would expect, is very like that of the Blackbird. The chief differences are the humerus, which remains practically constant in all stages except the earliest, and the manus, which does not become as short in the fledgling as it does in the Blackbird, being always longer than the humerus. The earliest embryo is younger than the earliest Blackbird, but though considerable changes take place during this period, they are what one would expect from the known part of the embryonic development of the Blackbird, and it is probable that they occur in this species also.

Text-figure 6.



Wing-development of Song Thrush.

IV. Discussion of Wing-developments.

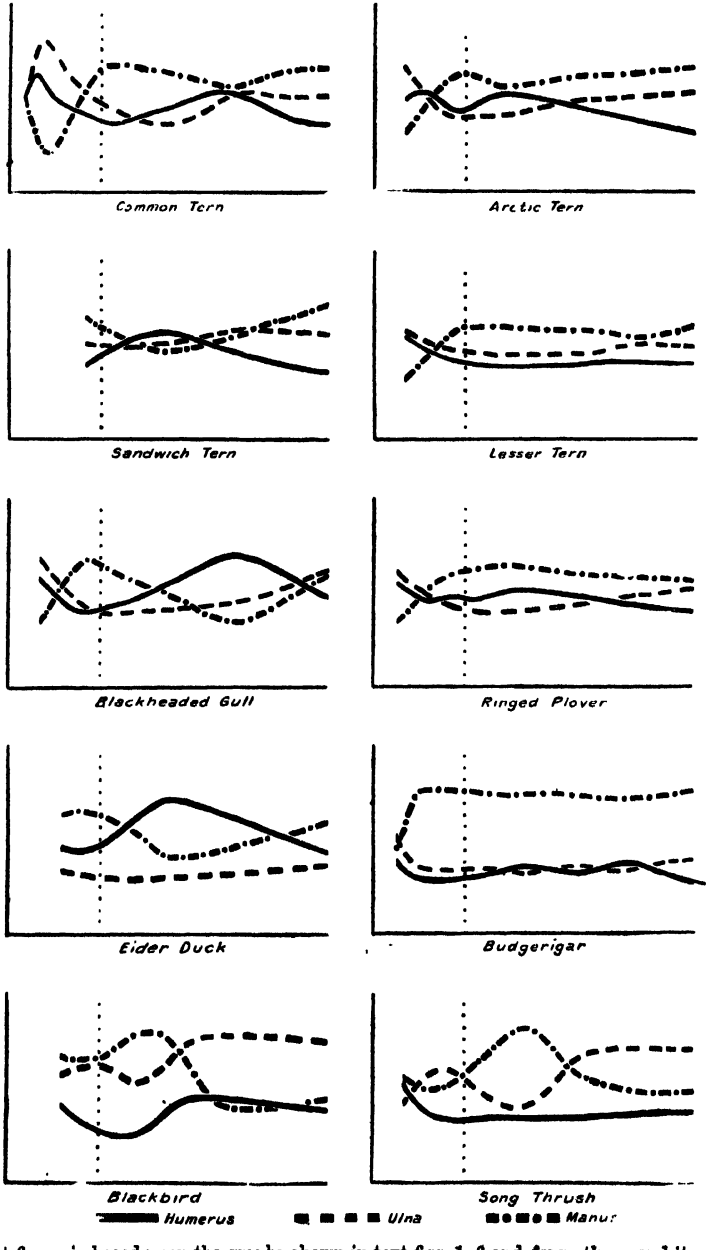
In discussing the changes in proportion which take place in the wings of these ten species during development there are several points which must be considered. Certain changes in proportion may take place of necessity during the development of all wings owing to the growth of the feathers or some such factor. Allied species may have a similar type of wing-development differing more or less according to the degree of relationship; or the changes may be related to special conditions of development or to the phylogenetic history of the wing. (See text-fig. 7.)

The first suggestion seems to be negatived by the Budgerigar, the proportions of whose wing remain practically unchanged from a very early embryonic period to the adult. There does seem to be a tendency, in the other species, for the manus to increase in the late embryonic or early nestling period, where it reaches a maximum and decreases again, but in the Budgerigar the increase in the manus takes place at a much earlier stage, and there is no decrease.

It might be expected that there would be an increase in the manus about the time of the development of the primary feathers in order to accommodate these. The Terns, Gull, Plover, and Duck are nidifugous species, and the young ones, in which the flight-feathers are not yet developed, have a covering of down, while the Budgerigar, Blackbird, and Thrush are nidicolous, and begin to develop these feathers at a much earlier stage. There does not, however, seem to be much difference in the time at which the increase in the manus takes place during development, and therefore it appears that there is no special increase in the manus parallel with the development of the feathers.

The ten species dealt with here belong to four orders. The Terns, Gull, and Plover belong to the Charadriiformes, the Eider Duck to the Anseriformes, the Budgerigar to the Cuculiformes, and the Thrush and Blackbird to the Passeriformes.

Text-figure 7.



This text-figure is based upon the graphs shown in text-figs. 1–6 and four others, and it expresses diagrammatically the changes in relative proportions of the wing-bones during development. For fuller explanation see text-fig. 1.

Of the Charadriiform species, the Terns and Gull belong to two subfamilies of the Laridæ, the Ringed Plover to the Limicolæ, and their types of wing-development appear to bear out these relationships. The Terns with their specialized wing, characterized by its long manus, all have very similar wing-developments, while that of the Gull differs from them slightly and the Plover to a greater extent. They are, however, all of the same type, with its increase of the manus and decrease of the ulna and humerus in the embryonic period and increase of the humerus in the nestling. It may be mentioned that four stages of the Wood Pigeon *C. palumbus*, have been measured, and it is interesting to see that what little of its development is known resembles that of a Tern, as does its adult wing. It is hoped in the future to work out its wing-development in detail.

It should be pointed out that the first two stages of the Common Tern are younger than the earliest stage of any of the other species. The changes in proportion during corresponding periods are very similar in all the Charadriiform species, and it seems likely that the abrupt change in the rate of growth of the ulna and manus seen in the earliest stages of the Common Tern occurs in all of them. It is hoped in future to verify this, and in the Common Tern to establish a number of other points in the region where this abrupt change in the rate of growth takes place.

The adult Eider Duck has a very different type of wing from the other species and a different type of development, owing to the persistence of the short ulna from the late embryo onwards. The other two orders have their own type of development, the Budgerigar being characterized by the constancy of the three lengths and the great length of the manus, the Thrushes by the variations of the ulna and manus.

The present evidence does seem to point to there being a distinct type of wing-development for allied species of birds, and it would be of great interest to work out the development of a larger number specially chosen to throw light upon this subject. It is hoped in the future to be able to do this. It would be important to obtain the wing-development of one of the Auks. They are characterized by having a short ulna, and, as this is also found in the Eider Duck, it would be specially interesting to determine whether their development is like that of the Duck or like that of the other Charadriiformes.

V. The Measurements of Adult Wings.

The adult birds whose wings have been measured are purely a random sample, consisting of all the birds' skeletons which happened to be available, and it is impossible to draw any definite conclusions from the present data owing to the small number which have so far been measured. When the work on wing-development was begun it naturally directed attention to the proportions of the adult wing and their variation from one species to another, and these measurements were taken in the hope of throwing some light on the subject. In discussing them, the lengths of the parts will be given as a percentage of the total length of the wing, and only the humerus, ulna, and manus are considered at present, though all the bones were measured.

Among these eighty wings there are remarkable variations in the lengths of the parts; for instance, the humerus of the Swift is 15·0 per cent., while that of the Little Grebe is 38·0 per cent; the ulna of the Guillemot is 27·4 per cent., while that of the Green-billed Toucan is 42·2 per cent.; and the manus of the Albatross is 25·3 per cent., while that of the Swift is 58·8 per cent. These are the extreme measurements for the different segments, but it is more important to consider the lengths of the parts in the same wing. Some species have all three parts about the same length, as, for example, the Arctic Skua—humerus, 33·3; ulna, 33·8; manus, 32·8 per cent.—but all other arrangements are found, and examples of some of them are afforded by the species used for the wing-development work. It may be

noted that, while there are a good many species, which have the lengths of the parts arranged in ascending order of magnitude, from humerus to manus, there are very few which have the opposite arrangement, with the lengths of the parts decreasing towards the manus. An example is the Little Grebe—humerus, 38·0; ulna, 33·9; manus, 28·1 per cent.

It is very difficult, except in a few cases, to find any relation between the proportions of the wing and the mode of flight or shape of wing. The wing of the Swift, *with its very short humerus and manus*, seems well adapted to its characteristic mode of flight, *and a similar wing is found in the* Martin, as one would expect, *though it is* not related to the Swift. The Terns also have the same type, though less exaggerated, and their wings have much the same long pointed shape. Here the proportions may show some correlation with the type of flight. The Budgerigar, however, has very much the same type of wing, its manus being the longest of all those measured except the Swift, but it has a short rounded wing and a whirring flight. The Wood-Pigeon is also very different from the Terns in its mode of flight and shape of wing, but in the proportions of its wings it is extremely like the Terns. (See Table I.)

TABLE I.

	Humerus.	Ulna.	Manus.
Swift, *Cypselus apus*	15·0	26·2	58·8
Sand-Martin, *Cotyle riparia*	21·9	34·5	43·6
Wood-Pigeon, *Columba palumbus*	29·2	32·0	38·6
Common Tern, *Sterna fluviatilis*	29·0	33·9	37·1
Arctic Tern, *Sterna macrura*	28·6	33·6	37·8
Sandwich Tern, *Sterna cantiaca*	27·5	34·1	38·4
Lesser Tern, *Sterna minuta*	29·2	33·3	37·5
Black Tern, *Hydrochelidon nigra*	28·1	32·9	39·0
Budgerigar, *Melopsittacus undulatus*	27·4	31·0	41·6

Of the wings measured, fourteen have a manus which is less than 30 per cent of the whole wing, and all but four of these are large birds, the exceptions being the Silver Pheasant, two species of Toucan, and the Little Grebe. There are only three conspicuously large birds which have been measured which do not come into this list. These are the Barnacle Goose, the Great Black-backed Gull, and the Gannet, and the Gannet is clearly of the same type, its manus being 30·5 per cent. There does seem to be evidence here that a short manus and a large size tend to go together, but on the basis of so few measurements as are at present available this can be no more than a suggestion to be verified in future.

TABLE II.

CORVINÆ.	Humerus.	Ulna.	Manus.
Raven, *C. corax*	28·8	35·3	35·8
Hooded Crow, *C. cornix*	29·0	35·3	35·6
Rook, *C. frugilegus*	29·0	35·2	35·6
Jackdaw, *C. monedula*	27·7	36·0	36·3
GARRULINÆ.			
Magpie, *P. rustica*	31·1	36·9	32·0
Jay, *G. glandarius*	31·9	37·0	31·1

The Toucans are notoriously bad fliers, and possibly their short manus is correlated with this. There does seem to be a tendency for birds of weak flight to have a short manus, to which the Hoatzin is an exception, since the parts of its wing are practically equal in length. The short manus of the Toucan might

possibly be associated with reduction of the wing, as it is the segment which is most reduced in flightless forms, and the Toucans, according to Beebe (1916), inhabit dense forest, remaining in a limited area and never flying far.

The present material affords several examples of allied forms having a similar type of wing. Seven species of the family Corvidæ have been measured, and they fall into two distinct groups (see Table II.). The members of the subfamily *Corvinæ* have a short humerus and the ulna and manus about the same length, while the *Garrulinæ* have a long ulna. The Terns and Auks are good examples, five species of each having been measured, each forming a compact group with a characteristic type of wing, and an interesting point is afforded by the Sparrow-Hawk, in which the male is considerably smaller than the female, but their wings are almost identical in proportions.

The Auks have a short ulna and a rather long manus, and it is interesting to see the same type of wing, only carried to a much greater extreme, in the Penguins, which are so closely convergent with the Auks in habits. The short ulna occurs in other aquatic forms, such as the Eider Duck, the Red-Throated Diver, and the Waterhen, and so may possibly be connected with the use of the wings in swimming. (See Table III.)

TABLE III.

	Humerus.	Ulna.	Manus.
Guillemot, *Uria troile*	36·2	27·4	36·4
Brünnich's Guillemot, *U. brünnichi*	34·3	29·2	35·3
Razorbill, *Alca torda*	34·5	28·0	37·5
Puffin, *Fratercula arctica*	35·4	28·0	36·6
Little Auk, *Mergulus alle*	34·3	28·3	35·3
Black-footed Penguin, *Spheniscus demersus*	32·6	25·3	42·0
Rock-hopper Penguin, *Eudyptes chrysocome*	31·2	24·5	44·1
Gentoo Penguin, *Pygoscelis papua*	33·0	23·5	43·4
Eudyptula minor	33·4	25·3	41·3
Red-throated Diver, *C. septentrionalis*	36·8	29·3	33·9
Eider Duck, *Somateria mollissima*	33·4	29·8	36·8
Waterhen, *Gallinula chloropus*	34·6	28·6	36·7

These resemblances of the wings of allied species suggest that a fuller study of the wings of a large series of birds from one group might be particularly interesting from the point of view of their phylogenetic relationships. Twenty-six species of the order Charadriiformes have so far been measured. The Auks and Terns, which are specialized groups, each has a characteristic wing, but the more generalized Charadriidæ and *Larinæ* have various types of wing, and the lengths of the parts are much less extreme than in the specialized groups. It is hoped that a more extensive study of the wings of these generalized groups may make it possible to determine whether these variations are due to different modes of flight, to some other factor such as the shape of the intact wing, or whether there can be a certain amount of variation independent of function. In this case one would expect the wings of the most closely allied forms to be the most similar. It is interesting to note that the wing of the Arctic Skua, a primitive member of the Laridæ, is similar to that of the Jacana, a primitive member of the Limicolæ, according to the measurements given by Beebe for the Jacana. All the parts of these wings are about the same length.

Beebe and Hartley lay stress upon the fact that in all the wings they investigated change in any segment was balanced by an equal and opposite change in one of the other two segments or by the sum of the changes in both of them. Naturally this occurs in the graphs because of the way in which the figures are calculated, the sum of the calculated lengths of the parts at any stage being equal

to the length of the adult wing. Then if one part increases there must be an equal decrease in the other two, since the sum is constant. It does not seem that this balance between the parts of the wing has any real significance, and though it is very striking in the graphs, this is merely a consequence of the way in which they are drawn.

The whole question of the proportions of the wing is so obscure at present, and so many striking exceptions arise in all attempts to correlate proportion with the mode of flight or any other factor, that it is impossible as yet to attempt any explanation. This paper can only serve to draw attention to the problem and form a preliminary study to further investigation along the lines indicated.

Summary.

1. The paper deals with the changes in proportion of the skeleton of birds' wings during development, and with the proportions of the skeleton of the wing in adult birds of different species.

2. The changes in proportion of the wing during development are described in ten species, belonging to four orders.

3. Allied species tend to have a similar wing-development.

4. There are no changes in proportion of the wing parallel with the development of the flight-feathers.

5. The proportions of the wing in adult birds in some cases may be related to the mode of use, but in the great majority the significance is not apparent.

6. Allied birds seem to have some tendency to have a similar type of wing; this may be due either to similar habits or to their relationship.

7. Large birds tend to have a short manus.

8. In view of the above results it would be extremely interesting to investigate similar measurements in the cases of some of the flightless birds.

9. No definite conclusions can be drawn from the data so far obtained. The paper is to be regarded as merely drawing attention to the problem and pointing out lines of investigation which it is hoped to pursue in the future, and the above conclusions are more suggestions than ascertained facts.

References.

Beebe, C. W., & Hartley, G. I. (1916.) Tropical Wild Life in British Guiana. New York Zoological Society, 1917.

Evans, A. H. (1898.) Cambridge Natural History, vol. Birds.

Latimer, H. B. (1927.) Post-natal Growth of the Chicken Skeleton. Amer. Journ. Anat. xl.

Parker, T. J. (1891.) Some Observations on the Anatomy and Development of *Apteryx*. Phil. Trans. Roy. Soc., B, clxxxi.

48. The Structure and Life-history of *Sciara nitidicollis* Meig. (Diptera).

By Iuan Thomas, M.Sc. (Wales) *.

(Department of Agricultural Entomology, University of Manchester.)

[Received July 2, 1930; Read November 18, 1930.]

(Text-figures 1–14.)

Contents.

	Page
I. Historical	1009
II. Description	1010
1. The Imago	1010
2. The Egg and Egg-laying	1012
3. The Larva	1013
4. The Prepupa	1023
5. The Pupa	1023
6. The Emergence	1025
III. Summary	1025
IV. References	1026

I. Historical.

Sciara nitidicollis was originally described by Meigen (12) in 1818. As regards the name of this species there is still some difficulty. The present situation is clearly represented in some of the remarks on the subject by Mr. F. W. Edwards †, of the British Museum :—" Lengersdorf has recently (Encycl. Ent. Diptera, v. p. 57, 1929) re-examined Meigen's collection, and states that the types of *nitidicollis* are not this species; but, on the other hand, the specimen labelled *pallipes* Fab. is the species which had previously been called *nitidicollis*. Lengersdorf does not say whether he proposes to adopt the name *pallipes* for your species; in another paper (Deutsch. Ent. Zeitschr. 1930, pp. 52–54) he states that *fenestralis* Zett., *sordidella* Zett., *pectoralis* Stæg., and *trivittata* Stæg. are synonyms, but I am not sure that he is right in regard to *pectoralis*. Of these names, the oldest is *fenestralis*, which must be used for the species if *pallipes* is not adopted. Other synonyms previously given by Lengersdorf (Verh. Nat. Ver. preuss. Rhein. u. Westf. lxxxi. p. 212, 1924) are *solani* Winn., *venusta* Winn., *velox* Winn., *humilis* Winn., *segnis* Winn., and *flaviventris* Winn."

Zetterstedt (22) records this species in his 'Diptera Scandinaviæ,' in which he gives a short description of both a male and a female. He gives the habitat " in graminosis et folliis fructicum." The species was first recorded in Britain by Walker (21) in 1856, in which account reference is made to the descriptions of Meigen and Zetterstedt, and a short description given. Schiner (19) has also

* This paper is part of a Thesis submitted for the degree of M.Sc. Wales. Communicated by Prof. J. S. Dunkerly, F.Z.S.

† Remarks quoted from a letter, by kind permission of Mr. Edwards.

recorded the species in his 'Fauna Austriaca.' Later descriptions and figures are those of Johannsen (6) under the synonym *S. paniciseta* Felt.

The writer does not think it necessary to redescribe the external adult morphology of the species because the above references may be supplemented by the excellent accounts of the head-capsule of Sciarids given by Frey (4) and Peterson (18) and a fur[illegible] (3).

From time to ti[illegible] ude o[illegible] e life tory, injury caused by, and [illegible] rva but, with the exception of Keilin's "note[illegible] found in Dipterous larvæ (7), little has been published on the anatomy of Sciarid larvæ since Osten Sacken (17) published, in 1862, a short description of Mycetophilid larvæ in general. Malloch (10) has given a very short description of the life-history of an unidentified species of *Sciara*, and Hungerford (5) has given an account of the habits, economic importance, and life-history of *S. coprophila*, but gives only a very short description of the external morphology of the larvæ (reference is made in this account to a paper by Bezzi (1) which has not been examined by the author). The most recently-published description of the larvæ of a Sciarid is that of Symes (20) on *S. præcox*? * Meig; but, as will be shown later, this account differs in many instances from observations made during this investigation, and the figures are only roughly drawn.

II. Description †.

1. *Internal Anatomy of Imago.*

Digestive System (text-fig. 1).

The *salivary glands* (*b*) are small and ovoid in shape; a number of small yellowish-brown reservoirs on both sides of the œsophagus lead into a common duct which passes to the base of the hypopharynx.

The *œsophagus* passes through the neck into the thorax, where it gives off a narrow duct which leads into a pyriform food-reservoir or crop (*c*). Vestiges of larval cæca (*e*) are present at the junction of the fore and mid intestines; this is also the point of attachment of the fatty bodies, which evidently correspond to the mandibular glands of the larva. There is a sharp contraction at the junction of the mid with the hind intestine; this is the point of entry of the four malpighian tubes, which are joined in pairs at their bases.

The hind intestine consists of an elongated narrow portion followed by a short, muscular, pyriform rectum.

Reproductive Systems.

The female genital system (text-fig. 2) is composed of two long ovaries, each of which leads into an oviduct which has a small dilation before it enters the common duct. Each immature ovary contains six rows of upwards of fourteen ovarioles, each containing an oöcyte. All the eggs appear to reach maturity at the same time. There are two large ovoid spermathecæ opening into two narrow ducts which unite a short distance before entering the vagina. The ducts of the two oval accessory glands also enter the vagina at this point.

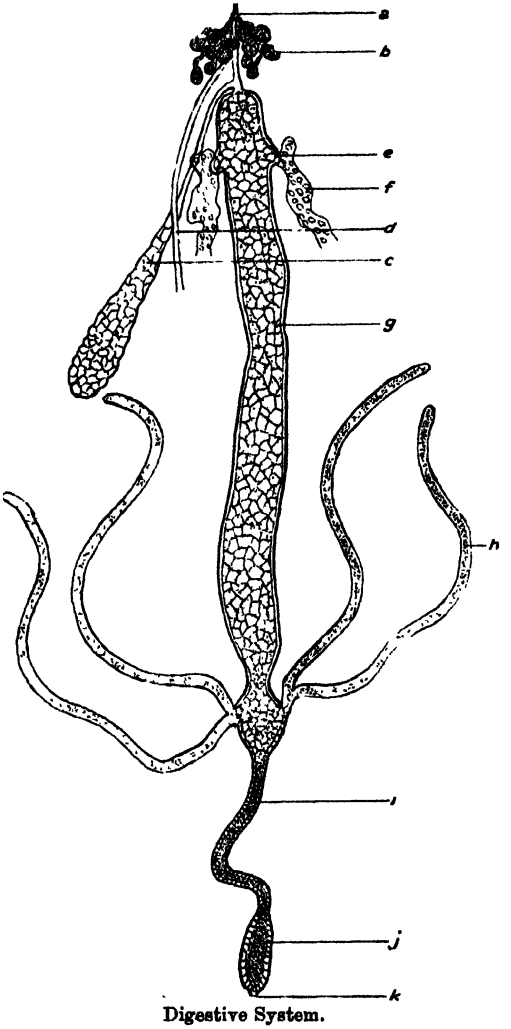
The *male genital system* (text-fig. 3) consists of two spherical testes from which vasa deferentia lead into a common duct. A small oval expansion occurs about half-way along this duct. Two ducts pass through this swollen portion, which probably acts as an accessory gland. From this point a short ejaculatory duct passes to the genital aperture.

* According to Edwards (3), the species described by Symes is *S. agraria* Felt.

† The writer is indebted to H. W. Miles for the use of his notes on *S. varians*? Joh.

The male, with wings spread and abdomen arched between its legs, runs up to the female from behind, with its claspers opening and shutting spasmodically: it

Text-figure 1.



Digestive System.

a. Œsophagus. *b*. Salivary glands. *c*. Food-reservoir. *d*. Dorsal vessel (heart). *e*. Vestiges of larval cæca. *f*. Fatty bodies. *g*. Mid intestine. *h*. Malpighian tube. *i*. Hind intestine. *j*. Rectum. *k*. Anus.

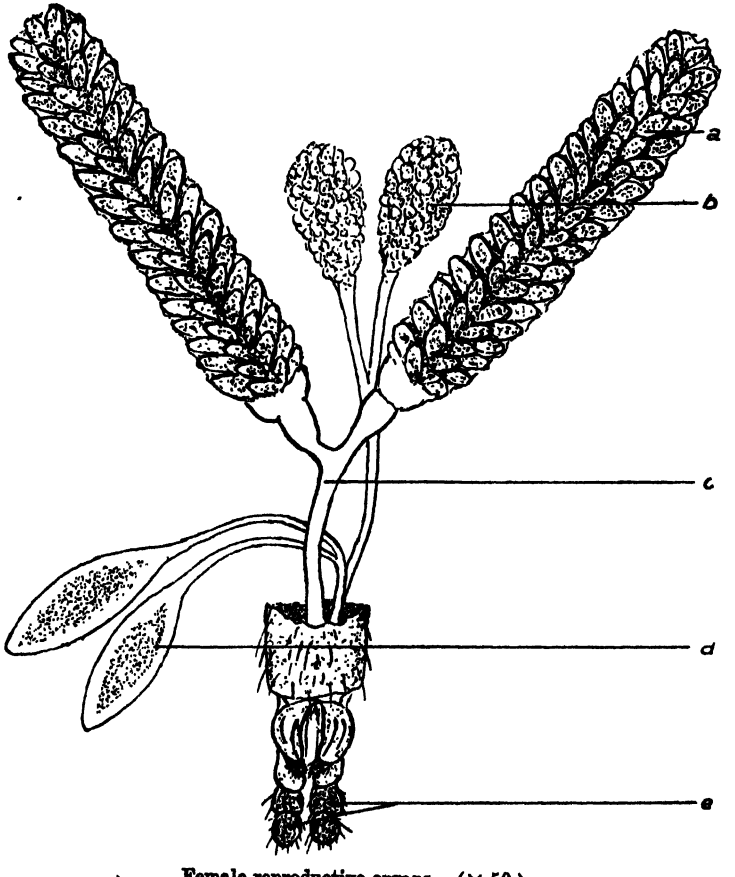
eventually grasps the end of the female abdomen and then turns over to face in the opposite direction to that of the female, thus bringing the genitalia into juxtapopisition. Mating occurs almost as soon as the flies have emerged from their pupal

cases, coition generally takes a few seconds, but may occasionally last as long as two minutes.

2. *The Egg and Egg-laying.*

Normally oviposition takes place about two days after coition; but, when mating has been long delayed, oviposition may take place within an hour. When ovipositing, a female searches for a small crevice with the tip of its abdomen, a deep moist crack being usually chosen. In captivity the flies oviposited freely on scarred and slug-eaten celery roots, potato tubers, cabbage roots, and tomato roots.

Text-figure 2.



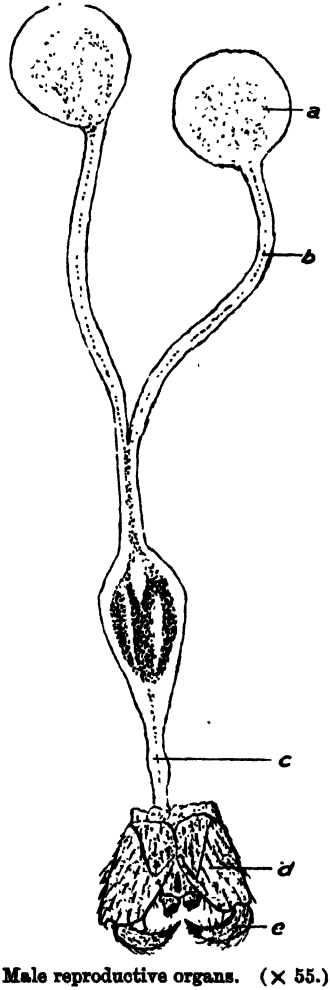
Female reproductive organs. (× 50.)

a. Ovary. *b*. Accessory glands. *c*. Oviduct. *d*. Spermathecæ. *e*. Cerci.

The eggs (text-fig. 4) are generally deposited in short strings of five to ten, placed end to end in succession. Occasionally the string is broken up and the eggs are found lying side by side. They are white and translucent, and adhere to one another by means of a translucent mucus by which they are covered. They measure 0·33 mm. by 0·71 mm., and are somewhat cylindrical in shape, with rounded ends. Moisture is essential for development, and under favourable

conditions all the eggs will hatch out. At the laboratory temperature, which varied from 5° C. to 22° C., the shortest time in which the eggs hatched out was six days. At a temperature which varied from 16° C. to 26° C. this period was shortened by thirty-six to forty-eight hours.

Text-figure 3.



Male reproductive organs. (× 55.)

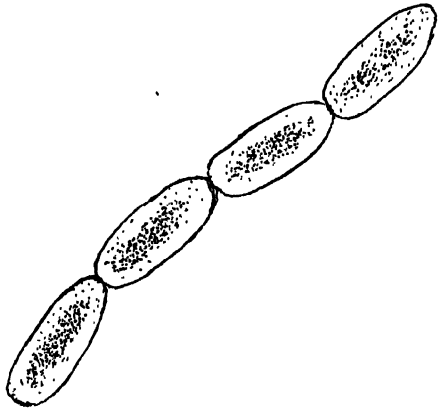
a. Testis. *b*. Vas deferens. *c*. Ejaculatory duct. *d*. Hypopygium. *e*. Claspers.

Development is rapid; the embryo is distinctly visible as a longitudinal black mass on the fourth day. By the seventh day the larval head is clearly differentiated, and the mandibles are seen to be continually opening and shutting.

3. *The Larva* (text-fig. 12)

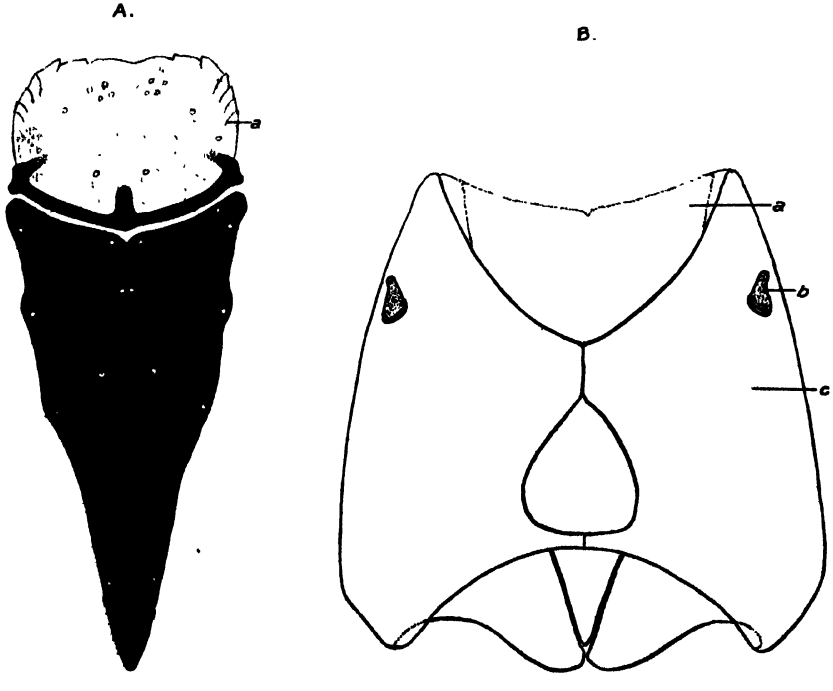
The newly-hatched larva measures 0·8 mm. to 0·9 mm. long, and the head measures about 0·08 mm. across. It resembles the adult larva very closely except

Text-figure 4.



Eggs. (× 29.)

Text-figure 5.

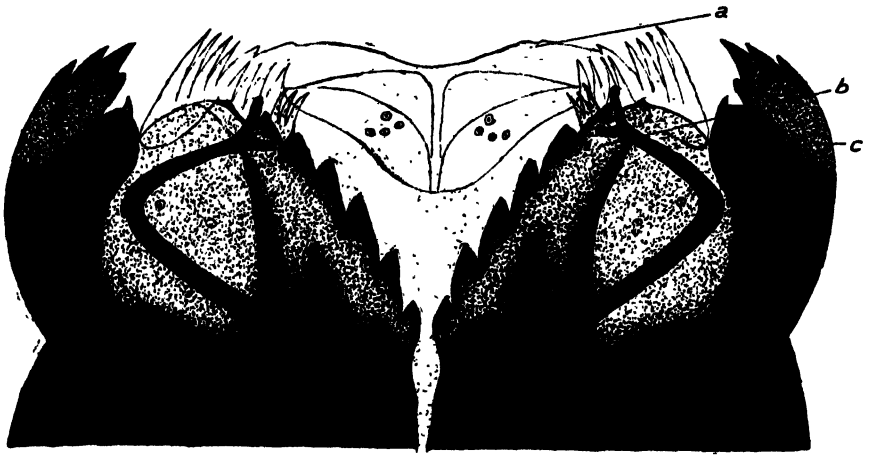


A. Dorsal sclerite of head capsule of larva, with *a*, the labrum (× 173). B. Head-capsule, ventral surface (× 173): *a*. Dorsal sclerite. *b*. Antenna. *c*. Latero-ventral sclerite.

in the fact that it has only one pair of spiracles; these are present on the prothoracic segment. The young larvæ commence feeding immediately after emergence, and, when disturbed, move rapidly away from the light. They become fully fed after eighteen to twenty days at laboratory temperatures.

The body of the fully-fed larva is elongate and subcylindrical, with twelve

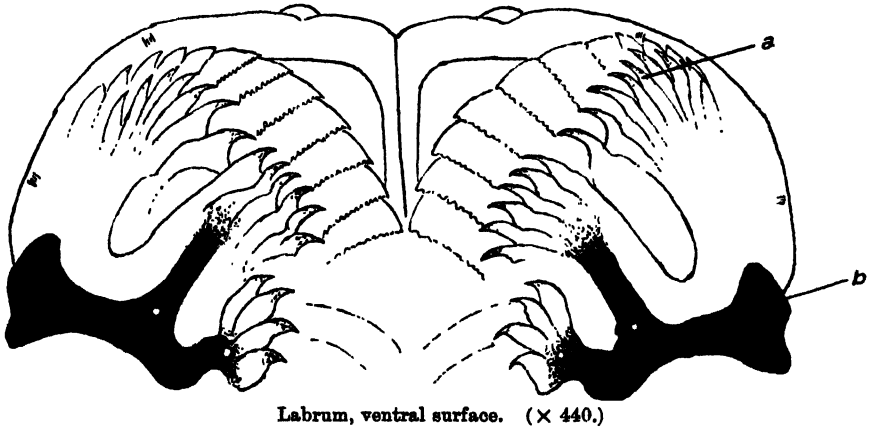
Text-figure 6.



Mouth-parts of larva. (× 360.)

a. Labrum. *b*. Maxilla. *c*. Mandibles.

Text-figure 7.



Labrum, ventral surface. (× 440.)

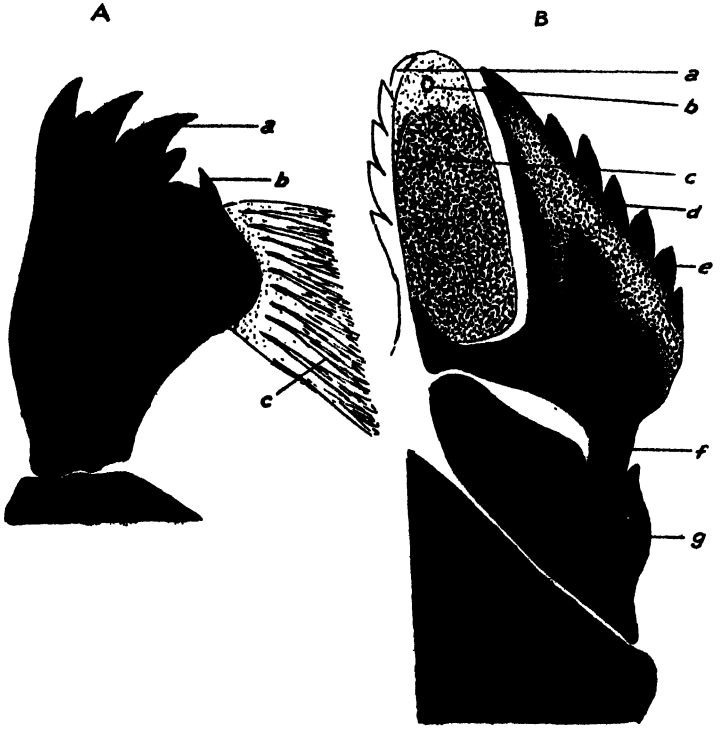
a. Fine claw-like bristles. *b*. Forked sclerite.

segments. The maximum length attained is 10 mm. The head is glossy black, complete, and strongly chitinized; the general shape is subquadrate. Balsam mounts of the head measure about 0·3 mm. long by 0·3 mm. across. There are three large chitinized sclerites (text-fig. 5)—two latero-ventral, and one dorsal in position. The former are connected on the ventral surface by an anterior wide

chitinized strip and a posterior strip which is very narrow. Viewed from the dorsal surface, the median dorsal sclerite is seen to be V-shaped, and is fused to the two lateral sclerites.

The *labrum* (text-fig. 7) consists of a strongly-chitinized basal sclerite which bears a thin membranous structure fringed on its ventral surface by minute claw-like bristles. The basal sclerite or "frame" fits closely on to the dorsal sclerite, and, when viewed from the ventral surface, it is seen that each side of the "frame" curves inwards and forks. The function of the labrum is noted by Osten Sacken (17):

Text-figure 8.



A.—Mandible (× 445): *a*. Apical tooth. *b*. Subapical tooth. *c*. Muscle of attachment.

B.—Maxilla (× 445): *a*. Membranous indentated sheath. *b*. Maxillary palpus. *c*. Outer lamella. *d*. Inner lamella. *e*. Teeth. *f*. Hinge, *g*. Cardo.

"it seems to be principally to shut the oral orifice, and perhaps to press on the mandibles and maxillæ during mastication."

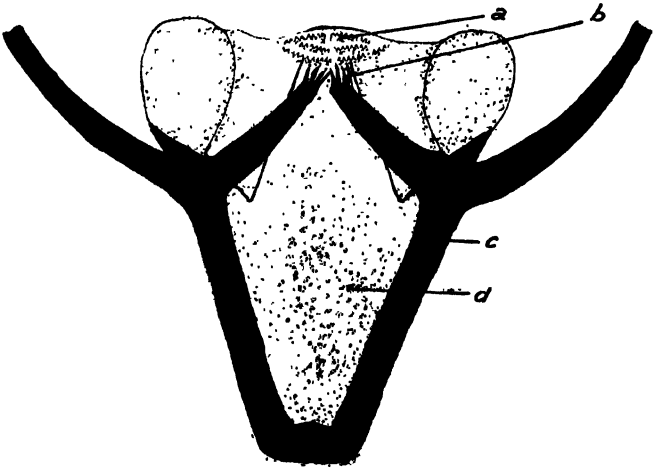
The *mandibles* (text-fig. 8 A) are attached to a small projection on the lateral sclerite, and are in a slightly oblique position. There are three large apical teeth and three small ones on the inner angle of the apex. The distal portion from which the teeth project is broad and has a distinct rounded projection on its inner edge, which bears the muscle of attachment. The articular basal portion is very narrow.

The *maxillæ* (text-fig. 8 B) are prominently placed, and are larger than the mandibles. There is a larger triangular basal sclerite or cardo on to which are attached two lobes—a strongly chitinized narrow inner lobe is closely applied to an outer lobe, which is flattened and less chitinized. There is no actual fusion between these two lobes, for slight pressure on a coverslip serves to separate them. The inner lobe is hinged to the cardo by a narrow strip of chitin; it is serrated on its inner surface, having seven distinct indentations. The outer lobe has a small fleshy palp near its distal end; this is visible as a round pellucid spot. A membranous indentated sheath is visible on the outer edge of the inner lobe.

The homologies of these parts have not been defined, but it is likely that the outer lobe, as a whole, is the maxillary palpus, the small pellucid spot being a partially atrophied distal joint. This is suggested by comparing the maxilla with the figure of the maxilla of *Bibio johannis* L. given by Morris (**13**); the inner lobe has been termed the mala.

The *labium* (text-fig. 9) is situated between the maxillæ; it is a V-shaped struc-

Text-figure 9.



Labium.

a. Rows of very fine teeth. *b*. Bristles. *c*. V-shaped sclerites. *d*. Membrane.

ture, which according to Osten Sacken is probably used in connection with the cocoon-spinning of the larva. No adequate description or figure, however, is given. An inner and an outer rod of chitin arise from the branch of the V on either side. The function of the outer rod is probably to keep the labium in position. A very thin membrane is spread between the forks of the V; this bears on its inner surface at the distal end three rows of exceedingly short, fine, tooth-like bristles.

The antennæ are sessile and very rudimentary; they occur on the ventral surface of the lateral sclerite just posterior to the point at which the mandibles are hinged. I could not detect a pellucid clear spot or ocellus below the antenna.

The *body* of the larva is translucent and footless; Johannsen (**6**), in referring to the characters of Mycetophilid larvæ in general, states that "the larva is without hair or bristles except that in some genera there are two transverse rows of simple or bifid ambulacral setulæ on the margin of each abdominal segment on the ventral side." However, there are present on the larva of *S. nitidicollis*, on the ventral surface, at the junction of each segment, about twenty to twenty-five rows of

minute chitinous processes directed backwards and visible only under high magnification. There are also present on the thorax minute "leg hairs" similar to those on the larva of *S. medullaris* described by Keilin (**6** *a*). These are exceedingly short, rigid, sensory hairs situated latero-ventrally; there are four hairs, arranged in two series, in the position of each atrophied thoracic leg of the larva. The twelfth segment is curved ventrally to act as a pseudopod; this, together with the chitinous processes, forms the means of progression of the larva. There is a well-developed peripneustic tracheal system with eight pairs of spiracles—one pair of prothoracic and seven on the first seven abdominal segments. They are small and rounded and situated laterally, similar in shape and brown in colour except the prothoracic, which is slightly larger, and situated in a more dorsal position than the abdominal spiracles.

Internal Structure of the Larva.

The Alimentary Canal (text-fig. 10).

The *pharynx* leads into a narrow *œsophagus* which, after a short distance, is surrounded by a large œsophageal valve: this has well-developed annular and longitudinal muscles. There is a sudden transition from the epithelium of the œsophagus to that of the mesenteron; the internal longitudinal muscles of the œsophagus pass through the annular muscles to become external on the mesenteron.

The *mesenteron* is of very simple construction, being a straight tube which extends to the end of the eighth segment. It is succeeded by the intestine, which may be divided into two tracts, the *colon* and *rectum*. The walls of the colon during the first part of its course are very muscular and capable of dilation; they gradually thin out to become very flexible. There is a sudden expansion into a wide rectum, the muscles near its termination become thickened, and the cavity becomes smaller, to open out at a very narrow anus.

Four long *Malpighian tubules* open into the alimentary canal at the junction of the mesenteron with the colon; each runs forward for a short distance and then curves backwards to end blindly in the last segment.

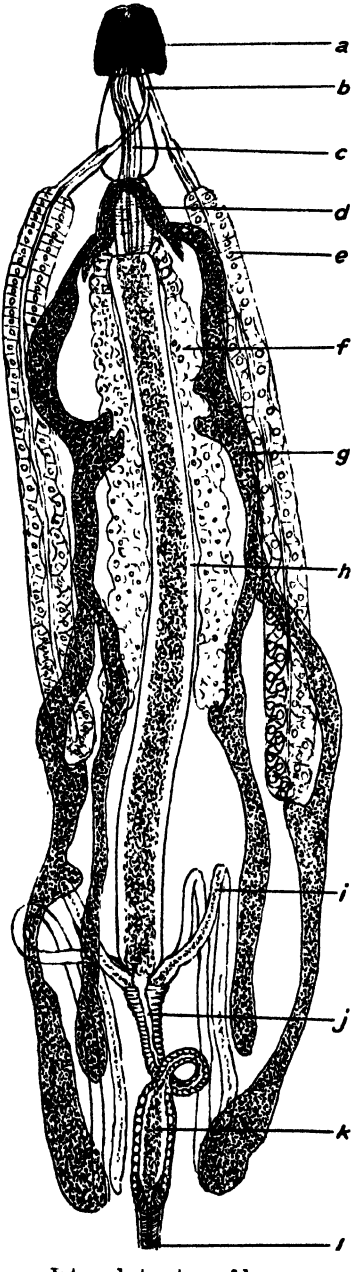
Glands (text-fig. 10).

Two long salivary glands lie one on either side of the alimentary canal. A narrow canal is enclosed by an epithelial layer of cells with large nuclei; these cells are very narrow in the anterior region of the gland, but become elongated in the posterior region to enclose an irregular reservoir. The glands pass into narrow ducts which unite in the region of the subœsophageal ganglion to enter the floor of the mouth.

Two cæca are connected with the alimentary canal in the region of the œsophageal valve. These extend backwards for two-thirds of the length of the stomach; they are highly nucleated and spongy in appearance.

In addition to the above there are two *mandibular glands*, a short description of which has been given by Keilin (**7**). They enter the mouth at the base of the mandibles and extend the whole length of the body. The ducts are very narrow and only just visible under the high power. Each gland is attached near its anterior end to the œsophageal valve; from this point it curves over the dorsal surface of the alimentary canal and divides into two long cæca about half-way along the length of the mesenteron. Two of these branches terminate in the tenth segment and two extend along the length of the mesenteron. Although these glands are large and take up a large amount of the body-space of the larva, Symes (**20**) has not represented them in his figure of the "alimentary tract and glands of *S. præcox*." He states later, however, that "the body cavity is densely packed with fatty tissues." These are, in all probability, the mandibular glands. In addition to the larva of *S. nitidicollis*, I have examined the larvæ of *S. aurifila* Winn. and *S. varians*?

Text-figure 10.



Internal structure of larva.

a. Head. *b*. Salivary duct. *c*. Œsophagus. *d*. Œsophageal valve. *e*. Salivary gland. *f*. Cæcum. *g*. Mandibular gland. *h*. Mesenteron. *i*. Malpighian tubes. *j*. Colon. *k*. Rectum. *l*. Anus.

Joh., and in each case these glands were present and almost identical with those of *S. nitidicollis*; in fact, the only difference I could detect between the larvæ of these species was that of size. Symes (20) has figured the head of the larva as being as broad as the body, even after dissection, and the salivary glands as reaching a point posterior to the point of attachment of the malpighian tubes. This again is improbable, as in all the species I have examined the salivary glands (unless they were stretched during the process of dissection) were only slightly longer than the cæca of the alimentary canal.

The Nervous System (text-fig. 11).

The *brain*, or *supraœsophageal ganglion*, is two-lobed, and actually lies in the anterior region of the prothoracic segment. Two fine *œsophageal connectives* pass round the œsophagus to connect with the anterior end of the large *subœsophageal ganglion*. The head being almost completely filled with the muscles of the mouth-parts, the brain has been pushed back into the first segment.

There are three thoracic and eight abdominal ganglia. The first thoracic ganglion lies immediately behind the subœsophageal ganglion and just inside the first segment of the larva. The second thoracic lies equidistant from the anterior and posterior margins of the second segment, and the third thoracic lies just inside the third thoracic segment near its anterior margin. All three thoracic ganglia are joined to one another, and the third thoracic is joined to the first abdominal ganglion by distinct double connectives.

The first to the sixth abdominal ganglia lie in the abdominal segments 1 to 6 respectively, and in a similar position to that of the third thoracic ganglion; the seventh and eighth abdominal ganglia lie on the junction of the sixth and seventh and seventh and eighth abdominal segments respectively. These ganglia are joined by double connectives which are fused to form apparently single connectives on leaving the preceding ganglion. The eighth ganglion gives off two comparatively large nerve-fibres directed posteriorly, these divide up into nerve-fibres in the region of the anus. Each ganglion is distinctly bilobed, and each lobe gives off a nerve, in a lateral direction, from a position about one-third of the length of the ganglion from its anterior end.

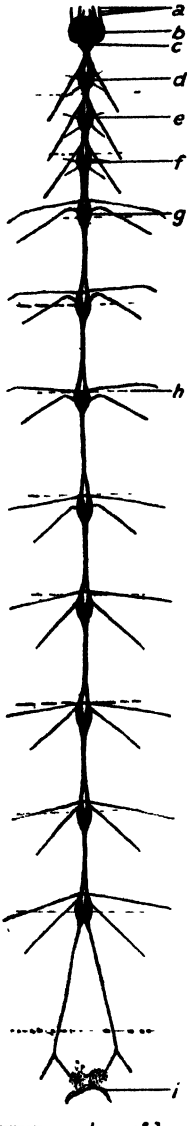
These observations agree with those of Symes (20) only in so far as the supra- and subœsophageal ganglia are concerned. In describing the nervous system, Symes (20) states that "the nervous system is composed of eight ganglia, two large ganglia just behind the head representing the supra-and subœsophageal ganglia, and six in the body." This is probably an inaccurate observation, as in all the Sciarid larvæ examined by the author the nervous system was almost identical with that described above. Morris (13), when discussing the affinities of the larva of *Bibio johannis* L., states that "it bears a closer resemblance to the larvæ of Mycetophilidæ than to any other group. This resemblance appears to be due to the fact that the two families are phylogenetically closely related."

The accuracy of this statement is borne out by the present observations, for with regard to the nervous system in particular there is a very close resemblance between that of *B. johannis* L. and *S. nitidicollis*. The number of ganglia in the two species is identical; the whole system differs only in the position of the eighth abdominal ganglion. In *B. johannis* L., Morris (13) describes this ganglion as being in the posterior region of the eighth abdominal segment, whereas in *Sciara* it is situated on the junction of the seventh and eighth segments.

The Tracheal System (text-fig. 12).

Two main longitudinal tracheal trunks extend almost the whole length of the body of the larva. From the prothoracic spiracle a branch runs in to connect with the main trunk from one side; from this point one branch runs forward into the

Text-figure 11.



Nervous system of larva.

a. Cephalic nerves. *b*. Supracesophageal ganglion. *c*. Subœsophageal ganglion. *d*. First thoracic ganglion. *e*. Second thoracic ganglion. *f*. Third thoracic ganglion. *g*. First abdominal ganglion. *h*. Segmental division. *i*. Anus.

head and one curves ventrally to divide into a ventral branch and a branch which is a part of the secondary longitudinal system. The main trunk passes backwards and gives off two ventral branches, one into the second and one into the third thoracic segment. In each of the first six abdominal segments the system is

Text-figure 12.



Tracheal system of larva. (× 17.)

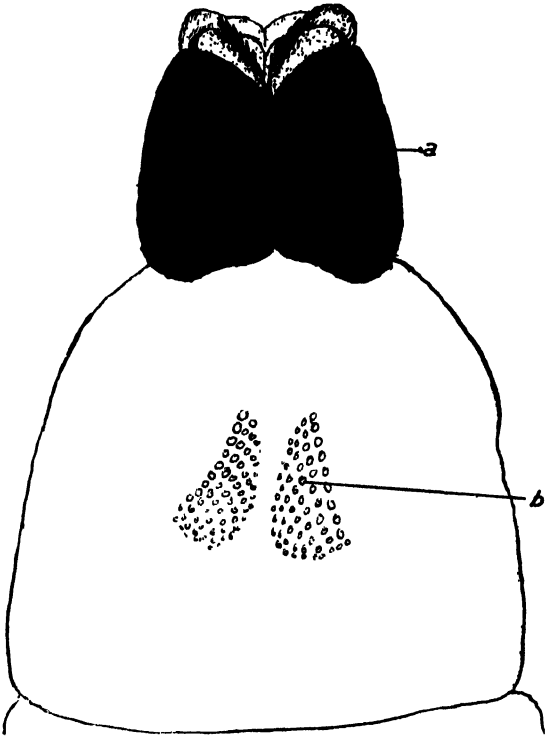
a. Head. *b*. Prothoracic spiracle. *c*. Secondary longitudinal system. *d*. First abdominal spiracle. *e*. Main longitudinal trunk. *f*. Seventh abdominal spiracle. *g*. Transverse connective.

similar, consisting of a main trunk, a ventral branch, a small dorsal branch, and a branch opening out at the spiracle. Posterior to the last abdominal spiracles a transverse branch connects the two lateral trunks; beyond this point the main system splits up into tracheal capillaries.

4. *The Prepupa* (text-fig. 13).

When fully fed the larva becomes sluggish, and for about two days works at the construction of a crude pupal shelter or cocoon. This is built of minute pieces of material on which the larva has been feeding, bound together by very fine silk-like

Text-figure 13.



Prepupa. (× 110.)

a. Head. *b*. Imaginal eyes.

threads. After a period of quiescence lasting about twenty-four hours, during which the larva becomes shorter and stouter, imaginal eyes (text-fig. 13) can be seen as small, triangular, spotted areas visible through the chitin of the prothoracic segment: finally the larval skin is cast off to reveal the pupa.

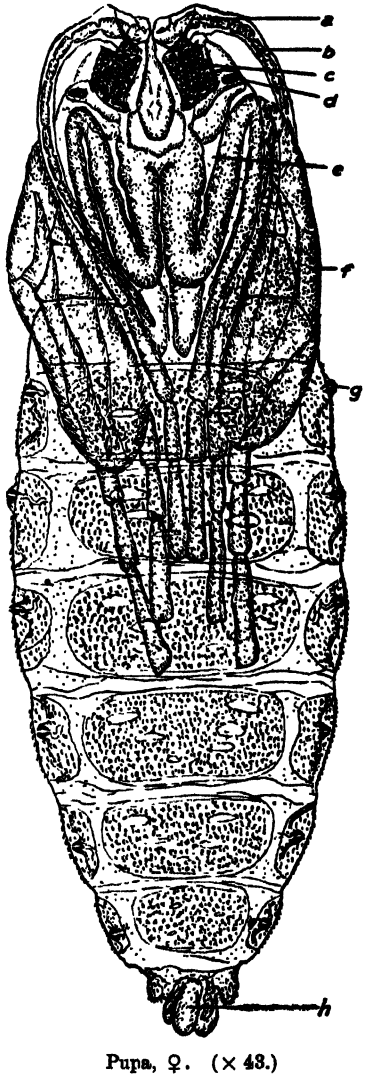
5. *The Pupa* (text-fig. 14).

The pupa is obtect and measures about 2·6–3·2 mm. in length. It is at first yellow or cream-coloured, becoming brown in a few days and finally black. There are two short, curved, pointed processes on the dorsal surface of the head and a small expansion at the base of each antenna. The antennæ are bent around the eyes, their distal portions resting on the ventral surface of the pupa. The legs are closely applied to the ventral surface; the tarsi of the posterior pair extend as far as the fifth abdominal segment.

The prothoracic spiracle is large and placed on a small projection a short

distance above the base of the wing. There are six pairs of abdominal spiracles. The female in the pupal stage is easily distinguished by the large size of its abdomen.

Text-figure 14.



Pupa, ♀. (× 43.)

a. Dorsal bristle. *b*. Antenna. *c*. Eye. *d*. Prothoracic spiracle. *e*. Prothoracic leg. *f*. Wing-sheath. *g*. First abdominal spiracle. *h*. Genitalia.

The duration of the pupal period under laboratory conditions is twelve to fifteen days; at a temperature varying between 15° C. and 26° C. the period was shortened to eight days.

6. *Emergence.*

Before emerging, the pupa works itself forward out of the cocoon until only the last three or four abdominal segments are left inside. On drying, a split occurs along the dorsal surface of the pupal skin. The imago works itself forward in the pupal skin by convulsive movements of the abdomen until its head and prothorax are extruded; at this stage the head is bent forward on the thorax. The head is now lifted and the antennæ are drawn out from their sheaths. The legs and wings are drawn upwards until the wings become free; immediately this happens the prothoracic legs are pulled up to rest on the outside of the pupal case, the abdomen is stretched out inside the pupal case, and there is a discharge of rectal fluid. This is followed by a contraction of the abdomen, and after a short period of violent activity the insect is free.

The wings on emergence are folded, and extend only as far as the third abdominal segment. The newly-emerged insect runs about, pausing frequently in efforts to distend its wings, which become fully expanded after approximately half an hour.

The shortness of the period taken by the species to complete its life-cycle is emphasised if the various stages are tabulated as follows:—

Egg	Hatches in 6–8 days.
Larva.....	Fully fed after 18–20 days.
Prepupa.....	Constructs cocoon in 1 day.
,, ...	Period of quiescence 2 days.
Pupa	Imago emerges after 8–15 days.
Imago	Oviposits after 1–2 days.

From the above table it is seen that, under laboratory conditions, the shortest life-cycle of this species is complete in thirty-six days.

These times agree very closely with those obtained by Symes (**20**) for *S. præcox* Meig., but differ widely from those for *S. coprophila* given by Hungerford (**5**):—

	S. præcox.	*S. coprophila.*
Egg	5–7 days	6 days
Larva..... ...	19–32 days	11–12 days
Prepupa.....	——	1 day
Pupa	8–11 days	5–6 days
Imago	1 day	1 day

The shortest period for *S. præcox* is thirty-three days and for *S. coprophila* twenty-four days.

III. Summary.

The species *S. nitidicollis* was bred out from decaying celery roots. The synonomy has been discussed and reference made to the original and subsequent descriptions of the fly. An account of the life-history has been given, together with descriptions of the various stages and the times taken in the different stages. After a short description of the adult the life-history is described, beginning with the egg-stage.

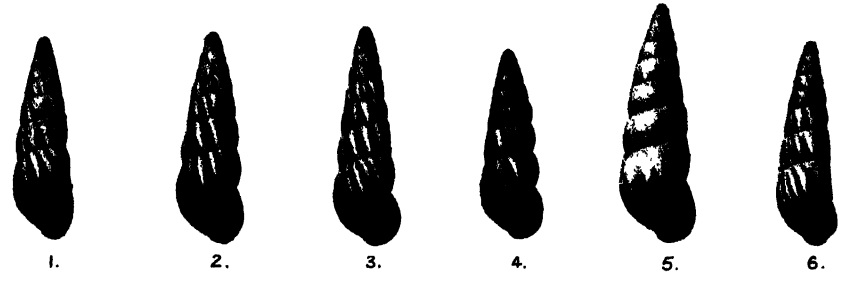
The author is indebted to Professor J. S. Dunkerly and Mr. H. W. Miles for helpful criticism and advice, and to Mr. F. W. Edwards, of the British Museum, for identification of the material and for very valuable criticism.

IV. References.

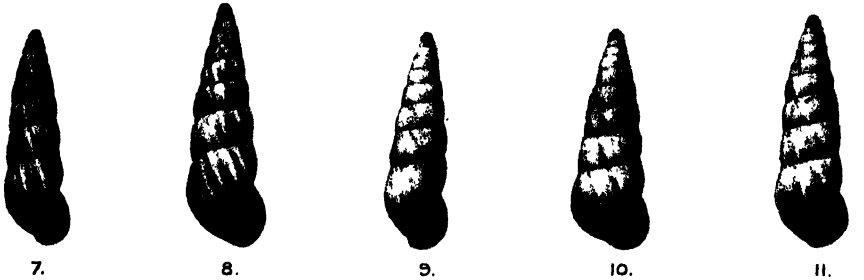
1. Bezzi, M. G. G. (1904.) Contribuzione alla conoscenza della metamorfosi della *Sciara analis* Egg. Redia, xi. pp. 280–305, figs. 1–21.
2. Edwards, F. W. (1913.) Notes on British Mycetophilidæ. Trans. Ent. Soc. Lond. 1913, pp. 334 82, pls. xii.–xviii.
3. ——— (1924.) British Fungus-Gnats (Diptera, Mycetophilidæ). With a revised Generic Classification of the Family. Trans. Ent. Soc. Lond. 1924, pp. 505–670, pls. xlix.–lxi.
4. Frey, R. (1913.) Ueber die Mundteile der Mycetophiliden, Sciariden, und Cecidomiiden. Helsingfors Acta Soc. Fauna et Flora Fenn. xxxvii. (3) pp. 1–89, 3 Taf.
5. Hungerford, H. B. (1916.) *Sciara* Maggots injurious to Potted Plants. Trans. Econ. Ent. Concord N. H. pp. 538–49.
6. Johannsen, O. A. (1912.) Fungus Gnats of North America.—Pt. IV. Bull. Maine Exp. Stn. 200, pp. 57–146, 7 pls.

6*a*. Keilin, D. (1911.) Sur certains organes sensitifs constants chez les larves de Diptères et leur signification probable. C. R. Acad. Sci. cliii. pp. 977–79.

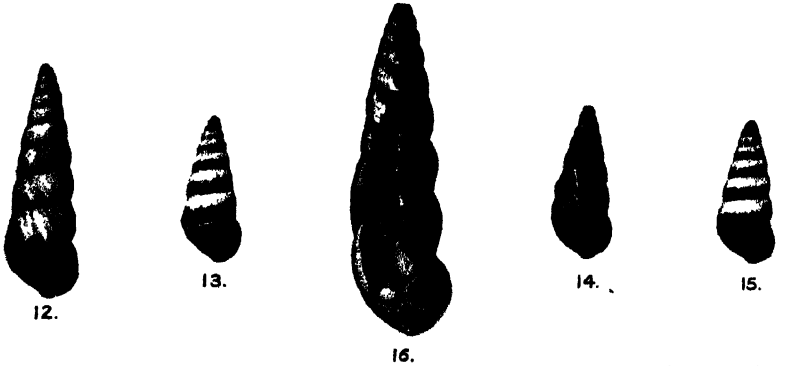
7. ——— (1913.) Sur diverses glandes des Larves des Diptères, Arch. Zool. Gen. et Exp. 52, 1.
8. ——— (1918.) Sur quelques modes particuliers de resistance des larves de Diptères contre la dessiccation. Bull. Soc. Ent. France, Mars 1918, pp. 102–104.
9. ——— (1919.) On the Structure of the Larvæ and the Systematic Position of *Mycetobia* Mg., *Ditomyia* Winn., and *Symmerus* Walk. (Diptera, Nematocera). Ann. Mag. Nat. Hist. (9) iii. pp. 33–42, pls. ii.–v.
10. Malloch, J. R. (1915.) Some additional Records of Chironomides for Illinois and Notes on other Illinois Diptera. Urbana Bull. Illinois Lab. xi. p. 320, figs. 1–4.
11. ——— (1917.) A Preliminary Classification of Diptera, exclusive of *Pupipara*, based upon Larval and Pupal Characters. Bull. Illinois State Lab. Nat. Hist. xii., iii.
12. Meigen, J. W. (1818.) Systematische Beschreibung der bekannten Europaischen zweiflügeligen Insekten, i. p. 281, 8.
13. Morris, H. M. (1917.) On the Larval and Pupal Stages of *Bibio johannis* L. Ann. App. Biol. iv. (3) pp. 91–114.
14. ——— (1918.) The Larval and Pupal Stages of *Scatopse notata* L. Ann. App. Biol. v. (2) pp. 102–11.
15. ——— (1921.) The Larval and Pupal Stages of the Bibionidæ. Bull. Ent. Res. xii. (3) pp. 221–32.
16. ——— (1921.) *Ibid.*—Part II. Bull. Ent. Res. xiii. pp. 189–95.
17. Osten Sacken, C. R. (1863.) Characters of the Larvæ of Mycetophilidæ. Proc. Ent. Soc. Phil. i. pp. 151–172.
18. Peterson, A. (1916.) The Head-capsule and Mouth-parts of Diptera. Illinois Biol. Mon. 3, 2, pp. 1–62, 25 pls.
19. Schiner, J. B. (1864.) Fauna Austriaca, xi. p. 422, 18.
20. Symes, C. B., & Chorley, J. K. (1921.) Insect Pests of Mushrooms. Fruit Gr., Fruiterer, Flor., & Mk. Gard. li. 1313, pp. 142–45; 1315, pp. 234–36; 1319, pp. 454–56; 1320, pp. 494–96, 7 pls., 23 figs.
21. Walker, F. (1856.) Insecta Britannica.—Diptera, iii. p. 52, 5.
22. Zetterstedt, J. W. (1851.) Diptera Scandinaviæ, x. p. 3737, 25.



1. 2. 3. 4. 5. 6.



7. 8. 9. 10. 11.



12. 13. 14. 15. 16.

John Bale, Sons & Danielsson, Ltd. London.

COCHLICELLA ACUTA.

49. The Natural History and Variation of the Pointed Snail, *Cochlicella acuta* (Müll.).

By D. Aubertin, M.Sc., A. E. Ellis, B.A., and G. C. Robson, M.A., F.Z.S.

(Plate I.* ; Text-figures 1 & 2.)

[Received May 31, 1930: Read November 4, 1930.]

Contents.

	Page
1. Introduction	1027
2. Procedure	1029
3. Shell-pattern and Structure	1030
4. Habits and Life-history	1032
5. The Geographical Distribution of the Patterns	1035
6. History of the Sussex Colonies	1037
7. Description of the Habitats of the Sussex Colonies	1039
8. Analysis of the Sussex Colonies	1041
9. The Problem of Melanism in *C. acuta*	1049
10. Summary	1052
11. Bibliography	1053

1. Introduction.

This paper embodies the results of a study of local and colonial variation in the Pointed Snail, *Cochlicella acuta* (Müll.), which we have conducted during 1927–1930. The mollusc in question is a representative of a Palæarctic genus of Helicid land-snails. It exhibits very remarkable and characteristic variation in the colour-pattern of the shell—variation, indeed, which obtained for it the name "*Bulimus variabilis*" from Hartmann (1821). It is distributed around the Western littoral of Europe, and passes along the north and south shores of the Mediterranean † about as far east as Palestine, and reaches the shores of the Black Sea.

The peculiar local distribution of this form in populous colonies, and the striking variation in colour-pattern, render it a suitable subject for research on local variation and race-formation.

The object of our studies was to ascertain to what extent separate but adjacent colonies ‡ of such an animal of sedentary habits and with no apparent contact between its colonies, show significant differences of an order that could be treated statistically; whether there is any regular and fixed relationship between degree of isolation and structural divergence; and whether such colonies remain stable over a given period of years.

At the present time, while we are still in ignorance as to how races and species arise, it is very desirable to obtain some positive facts as to the way in which variants are distributed in a limited section of a natural population and in what

* For explanation of the Plate, see p. 1055.

† Some French writers (Fagot (1883), Pallary (1909)) distinguish *C. acuta* and *C. barbara*. Whatever may subsequently turn out to be the right name of this form, we have absolutely no doubt that the circum-Mediterranean and British forms called *C. acuta* are identical.

‡ The term "colony" is used in this paper to designate any topographically isolated community of individuals of a species. In land-snails such colonies are found in self-contained topographical features such as hedge-banks.

circumstances of environment. We do not pretend that a single study based on one member of a large and diverse phylum can give us a universal rule. The interspecific divergences of birds, insects, marine worms, etc., probably follow peculiar and individual courses of their own which are not comparable with that found in land-snails.

The isolated or semi-isolated colony of a sedentary organism like a land-snail may be said to be a good example of the initial stage of that form of group-divergence that has given us races, varieties, and species. If we admit that the origin of a single new character or phase of a character is the first step in evolutionary divergence, the colony is about the first stage at which distinct groups composed of the offspring of more than a single union are developed and a large number of similar individuals segregated from other like aggregates. The constitution of such colonies, the amount of statistically "significant" difference between them, and the relation between such divergence and divergences in environment may give us a clue to the way in which larger groups are developed.

We say advisedly "may"! We do not regard it as at all proved that the colony or isolated community is always the forerunner of the race or species. The groups formed within a localized population may be subject to continual breakdown. The isolated unit of one year may be resumed into the general population in the next, either by the development of some means by which the members of one colony are intermittently transferred to another, or by the complete reunion of isolated colonies.

Studies designed to elucidate some of these questions have been undertaken on land-snails by Crampton (1916, 1925), Boycott (1919, 1927), Aubertin (1927), and Alkins (1928). The results of these enquiries will be discussed in due course.

In a work of this nature it is desirable to accumulate all information on the life-history and habits of the animal studied that will assist in interpreting the results. We have been at considerable pains to amass all the data we could on the distribution and variation of *C. acuta* over its entire range, as it has occurred to us that it is desirable to know (*a*) to what extent the localized population under review may exhibit, either in part or as a whole, any phases recognizable as "climatic" variation, which might be revealed from a study of the species over its entire range, and (*b*) what relation the variation of the Sussex colonies bears to that of the species as a whole.

We have also been drawn, through the obvious necessity of considering the age and origin of our colonies, into a rather detailed inquiry into the history of the species in the south of England. Here we have been brought up against problems intimately concerned with the nature and differentia of our colonies, but of a different order, and it has been found that the natural history of *C. acuta*, at least in so far as its distribution in southern England is concerned, presents some interesting problems of a special nature. These problems are by no means solved in this paper, and will require much further observation in the field.

The work was carried out on colonies of *C. acuta* found in Sussex at Saddlescombe and Rottingdean, near Brighton, and at Burpham, near Arundel. For the purpose of studying the broader features of variation in the species we have obtained specimens, either by personal collecting or by loan from collectors, from many places in the British Isles, continental Europe, and N. Africa. We are indebted to many friends for assistance in this work. Perhaps our greatest debt is due to Mr. H. S. Toms, who was the pioneer of the study of this species in Sussex. Dr. R. A. Fisher, F.R.S, has examined some of our figures, and has expressed his agreement with certain views set forth in section 8. We desire to acknowledge the assistance of Mr. H. W. Davies, Mr. O. W. Richards, Mr. R. Winckworth, Miss M. Strickland, and the Hon. Anne Palmer for kindly obtaining

various series, and of Dr. A. E. Boycott, F.R.S., Mr. C. Oldham, Mr. J. R. le B. Tomlin, Mr. J. W. Jackson, Mr. H. Watson, Major M. Connolly, and the Rev. S. Briggs for the loan of material. Miss Palmer, the Hon. L. Lindsey, and Lt.-Col. L. Baker kindly undertook a survey of different parts of Hampshire and West Sussex for us (see p. 1037). We are indebted to Captain S. T. Robson for the series of length-measurements mentioned on p. 1033, which will be published with other matter in a second contribution.

The expense involved in this study has been defrayed by a sum from the Government Grant Committee of the Royal Society, to which acknowledgment is hereby made.

2. Procedure.

C. acuta exhibits, as we have said, very extensive variation in colour-pattern. The size and proportion of the shell itself are variable, but in a less marked degree. We therefore selected the colour-pattern as the best-suited item for study. Our object, briefly stated, was to define the various pattern-phases, to discover in what percentage each phase was represented in certain colonies, and to find out by the usual statistical tests the significance of any divergences in percentage-incidence that might occur. Nine colonies in all were selected. Of these, two groups of four and two colonies were adjacent and almost contiguous, two more were distant, about 1 mile apart from each other and some 5 miles from the first. The ninth was about 15 miles from the preceding eight. Our colonies thus present a roughly-graded series with increasing distance apart, from which we might expect to ascertain if there is any relation between the amount of structural divergence and the degree of geographical separation.

The colonies selected were as follows:—Four at Saddlescombe (Nos. XXIX., XXX., XXXI., and XXXIII.), which is about 4 miles due north of Brighton; two (D.C.R. and XXV.) at Rottingdean and Saltdean; two just west of Rottingdean (LX. and LXI.), and one at Burpham, about 3 miles north-east of Arundel (XLVIII.). These eight colonies differ in the ecological nature of the habitat. The Saddlescombe colonies are from a downland roadside bank at an elevation of about 350 feet above the sea and 4 miles from the latter. The Rottingdean colony is from a flat turfy roadside about half a mile from the sea. The Saltdean colony is from a precipitous bank just above a low cliff 15 feet above high-water mark. The West Rottingdean colonies are from a roadside bank close to the sea. The Burpham colony is from the surface of a grass-field on an isolated spur of the Downs above the River Arun, about 5 miles from the sea. The exact ecological nature of each habitat, the flora, and the pH values of the soil are given in section 7. We need only say here that, of the Saddlescombe colonies, three are in habitats very similar to each other, ecologically considered, and one is in a rather different habitat. Those in the Rottingdean area and at Burpham are dissimilar *inter se* and from those at Saddlescombe. It will thus be seen that an opportunity is presented of studying any effect that environment may have in producing local divergences.

With the two-fold object of ascertaining what annual changes take place in the colonies, and of determining how far annual change may affect significant inter-colonial differences in any one year, we obtained two- and three-year series in most of our colonies, and samples from the colonies at D.C.R collected in 1920 and 1922 were lent us by Mr. R. Winckworth.

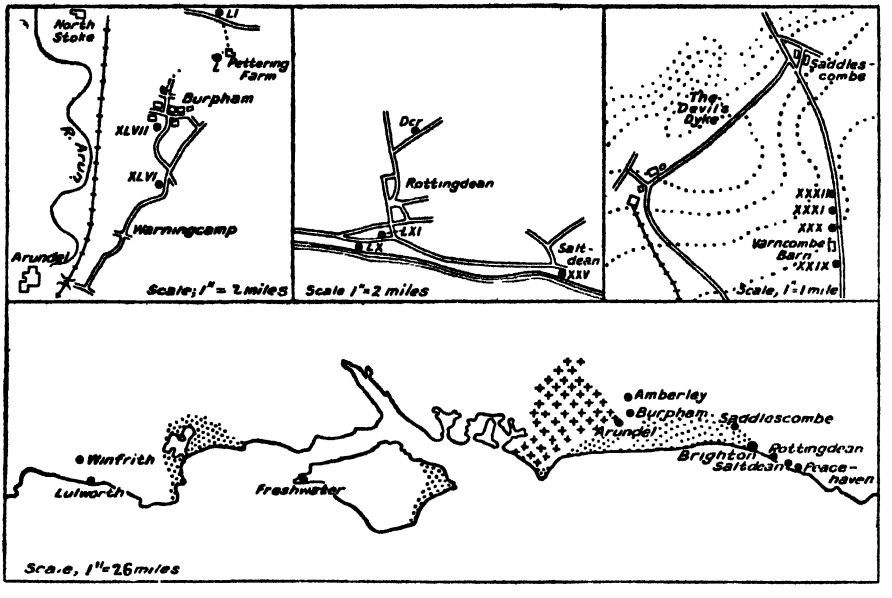
In all we examined 3527 specimens from the Sussex loci and about 3000 from other places in the British Isles and the Continent, some 6500 specimens in all.

For many reasons it would have been desirable to conduct breeding experiments with the various varietal forms. We were compelled, however, to limit our inquiry to the facts of variation, natural history, and distribution. We are able, however, thanks to the kindness of Mr. Hugh Watson, who has carried out

some genetical observations on the species, to include some useful and critical notes on this subject.

Some of the Saddlescombe animals were kept alive in specially prepared vivaria for about six months in order to study the growth-rate. The animals

Text-figure 1.—Map.



lived well in captivity, and we secured several broods of young from eggs laid in October.

The work of collecting the data and determining its significance (p. 1043) was undertaken by two of us working in common, so that a check was kept on the necessary determination of pattern and the calculations involved.

3. Shell-pattern and Structure.

(a) *Pattern.*—The shell of *C. acuta* is an elongate, rather narrow one, composed of nine whorls. It attains a maximum size of 26·5 mm. Its coloration and pattern consist of three main elements:—(*a*) Uniform white or faint straw ground-colour; (*b*) one or two dark bands seen externally on the last and penultimate whorl; (*c*) transverse markings of neat alternate stripes of white and brown ("flammulate").

The banded pattern and the flammulate are by no means uniform. The former occurs in the following phases:—

A. i. A single complete dark band.
 ii. A single broken band (a series of spots).
B. i. Two complete bands of equally intense colour.
 ii. Two bands, of which one is deep brown, the other a light chestnut.
 iii. One complete band, and the other broken into a series of spots or blotches.
 iv. Two broken bands.
 v. Two bands fused.

The flammulate pattern is seen in the following phases:—

(*a*) The dark stripes deep brown.
(*b*) The dark stripes pale brown.
(*c*) A series of three stripes (composed of a dark brown and a light brown stripe, followed by the original white "flammula"), or of two stripes (a brown and a "flammula").

The very remarkable amount of variation in the pattern of this form is due at the offset to the fact that the seven band-phases and the three flammulate phases unite to produce a great number of combinations. Thus the three flammulate types may be each found combined with one complete band, one broken band, two complete bands, or one complete and one broken band or two broken bands.

Many subordinate deviations from these primary phases and combination are found. Thus the two broken or complete bands may be separate or contiguous; one or more bands may combine with one of the flammulate phases and show an extension up each dark stripe; or again, in the flammulate dark form the "flammulæ" may practically disappear, leaving a melanic condition.

Toms (1922), who studied the large inland colony at Saddlescombe, proposed a classification of the permutations and combinations of the pattern-elements found there. He recognized 29 different forms, to which he gave varietal names. Reserving our opinion as to whether these should be recognized as taxonomic entities, we have largely adopted his basis of classification. In the material we have had under review we have recognized some 42 forms. It will be at once apparent to all who are familiar with colour-pattern in the molluscan shell that such items as ground-colour, the size of a band, or of the spots produced by the breaking-up of a band will be subject to much variation in themselves. In *C. acuta* the phases sketched above are readily discernible; but there is a large amount of subordinate variation which quite often renders it difficult or impossible to assign a given shell to a pattern-category. Our object being to study the percentage-incidence of colour-patterns in each colony, we found it necessary, having regard to the number of specimens available, to select a grouping of the patterns that corresponded with some well-marked genetic tendency and was sufficiently clear-cut to allow us to disregard the host of minute subdivisions that we obtained. It will be apparent, of course, that with samples averaging 160 specimens apiece the 40 categories discovered would not only be very cumbrous, but would produce (as we actually found) in many cases categories represented by so few individuals that the significance or non-significance of the corresponding percentage of patterns could not be satisfactorily tested. We therefore grouped our patterns in three main groups;—"A," unbanded (including flammulate and other non-banded types); "B^1," banded; and "B^2," banded and flammulate. These categories seem to us to represent definite varietal tendencies and to accommodate satisfactorily most of the intermediate forms which it would be difficult to place in a more finely-graded system.

b. *Shell-structure.*—We have examined transverse and longitudinal sections of the shell (prepared for us by Mr. R. H. Spires of the Geological Department of the British Museum) under a Zeiss binocular, 4 ocular × w.3 objective. We find the inner (nacreous) layer of the shell continuous and very largely unaffected by pigment-deposition. The outer (prismatic) layer in the flammulate forms exhibits differentiation corresponding with the superficial pattern. The deep layer under the white flammulæ appears as solid masses of unpigmented calcite. The flammulæ may be covered by the thin periostracal sheath that covers the whole shell, and is slightly tinted by pigment. The dark bands that alternate with the flammulæ are seen in section as masses of pigmented shell-substance that are clearly demarcated from the white areas, and pass down to come into contact with the nacreous layer. Whether these are masses of pigmented conchiolin

alone or whether they contain some calcite as well is uncertain, and there is no information in the literature of molluscan shell pigmentation to elucidate this point. In the banded form the area of the prismatic layer underlying the band or bands is exactly similar to that under the longitudinal stripes of the flammulate form, but the amount of pigment is usually greater, and it also seems to invade the nacreous layer.

A point of no little interest is involved in the question of the shell-pigment. Distaso (1908), who worked on the structure of the shell in *Cepea*, found in that form that there are two kinds of dark pigment—black and reddish. Görnitz (1923) has similarly distinguished between black (eumelanin) and reddish (phæomelanin) in the plumage of birds. Distaso found that it is the reddish pigment that forms the bands on the mantle, which nearly always correspond with the shell-bands. He does not specifically state that it gets from the latter into the shell-tissue; but it is a fair inference that it does so, and that the varying intensities of brown-black pigmentation are due to varying concentration of its granules. If this is true, and if the reddish pigment of the Pulmonata is in any way comparable to that found in birds, then there is a very curious difference in reaction between the molluscan and avian phæomelanin. Görnitz found that the phæomelanin of birds increased in dry conditions, whereas in *C. acuta*, at least, it is conspicuously reduced in dry areas (see p. 1049).

4. Habits and Life-history, etc.

The genus *Cochlicella* has been given a different status by various authors. Thus Pilsbry (1894) treats it as a subsection of *Helicella* (Helicidæ), and Ellis (1926) makes it a genus of that family equivalent to *Helicella*, *Theba*, *Helix*, etc. The peculiar structure of the reproductive organs seems to justify Ellis' choice. However that may be, the group, as at present known, consists of some seven species, all of which are of circum-Mediterranean distribution, principally occurring in the western end of the latter. *Acuta* may be regarded as the only true Lusitanian species, though *ventricosa* occurs in France and the Iberian Peninsula and *pringi* in the latter. All the species seem maritime in their habitat, and are especially found in the islands of the Mediterranean and N.E. Atlantic. *Acuta* is essentially an inhabitant of dunes, turfy cliffs, and hedge-banks, either at the very verge of the sea or within a few hundred yards of it. It is sometimes found in very inhospitable places of this kind. The colony from which we have obtained specimens on Tennyson's Down, just above the Needles (Isle of Wight), is an example of this. The animal was living there in practically naked chalk-rubble, or in the latter covered by a sparse mat of thin grass.

As *C. acuta* has this marked preference for maritime habitats, it is surprising to find that in three localities in the British Isles it has independently made itself at home at more or less considerable distances from the sea. In Ireland it occurs practically all over the country (Stelfox, 1911). In Dorset it is found 3 miles inland at Winfrith. In Sussex our Burpham colony is 5 miles from the sea, and that at Saddlescombe 4 miles.

Dupuy (1849, p. 313) speaks as though it was found more regularly away from the coast in France ("toutefois on le rencontre aussi dans l'intérieure des terres, mais plus particulièrement le long des fleuves." Germain (1908, p. 234) records permanent colonies in France (see below, p. 1039). In Spain Bofill and Haas (1920, p. 474) obtained it at Montserrat and other places far from the sea (*cf.* also Hidalgo (1875, p. 183)). The early record of Hartmann of its occurrence at Romanshorn (Switzerland) and at Freibourg (Breisgau) seems correct, but these occurrences are not given by Geyer (1927) in the modern German faunal list, nor by Mermod in his Swiss fauna (1930).

Although we admit that in one area at least there is good evidence for its accidental transport, which we believe must be facilitated by some special habit of adhesion, or else by the occupation of habitats from which accidental transport is more than usually feasible, we do not think this is the whole truth of these local invasions of inland habitats. It seems to us very unlikely that so plentiful and so widely distributed a form could escape accidental transport—*e. g.* in the south-west or north-west of England and Wales. Nevertheless, we have no evidence of its occurrence inland in these parts.

The species usually occurs in very great profusion, though in what one would call a "patchy" fashion. For example, one of us (G. C. R.) obtained it in 1929 in great numbers on rough dune-pasture west of the village of Paramé (Brittany), though it was but sparsely found in similar habitats eastwards of that locus. Some writers have noted a special preference on its part for certain plants (*e. g.*, Rzymowski, 1914), though in our experience it is tolerably eclectic in its tastes. The range of habitats is also wide, and includes pure dune with Marram (Marazion), dune-pasture (*passim*), dune-waste (St. Mary, Scilly Isles), chalk débris (The Needles), hedge-banks (Sussex), fallow fields (Burpham), and grass-plots (Rottingdean). As far as we can see it is, unlike many Pulmonates, neither crepuscular nor nocturnal. It may be found climbing actively on stalks and leaves at any time of the day. Nor is it, in our experience, so dependent on moisture as, *e. g.*, the Cepaeas. At least its activity is not so markedly associated with dew and rainfall.

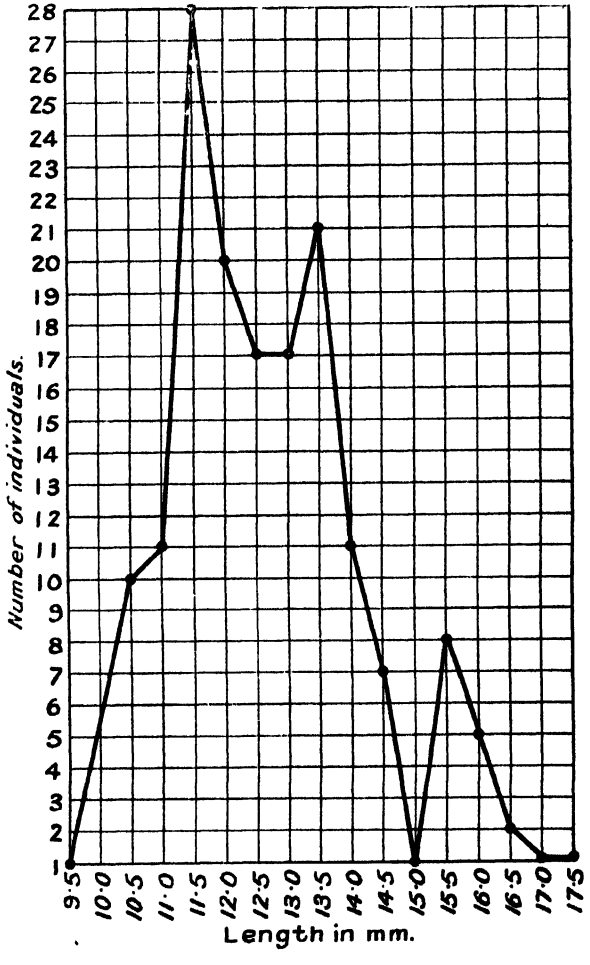
Breeding seems to go on from July until November. Our earliest annual record of couples taken *in coitu* in the field is in early July (1925, St. Mary, Scilly Isles), and we have records as late as the second week of November. Mr. H. S. Toms (MS.) believes that the principal hatching takes place in April, and that the animal becomes sexually mature in September. We found that in captivity eggs were laid as late as November. Toms (MS.) also believes that the majority of the snails of one year are killed or die off in the winter. There will be, no doubt, a heavy winter mortality; but there can be little doubt that *C. acuta* lives longer than one year. Data on this subject will be published in a later communication. It is enough at present to point out the following facts:—(*a*) The animals attain a maximum size of nearly 27 mm.; individuals of 20 mm. are fairly common, and the average size we have obtained in our colonies is 15 mm. In captivity healthy snails seem to put on about 2 mm. a month during the period of maximum growth. It would thus stand to reason that the snails born in June of one year would be about 12 mm. long at the beginning of the next year, and the forms averaging 15 mm., and often attaining 20 mm., must represent a population that survives from one year into the next. Actually a series obtained for us at Saddlescombe in April contained a large number of individuals, 14–16 mm. long, which are quite certainly young adults born in the previous year. (*b*) This conclusion is reinforced by the discovery, for which we are indebted to Captain S. T. Robson, who kindly undertook the necessary measurements, that each colony usually exhibits a bimodal length-curve (text-fig. 2) of such a nature as to suggest that each of our samples collected in October contains examples of two-year groups. More rarely there is evidence of tri-modality, suggesting that a few last over into a third year.

We feel thus justified in believing that *C. acuta* has an expectation of at least two years, though the heavy winter mortality probably kills off a high percentage each year.

As regards the intimate vital condition in which this form lives, very little can be said. Living as it does amid vegetation in banks and similar places, it is probably exposed to the attacks of field-mice, voles, and carnivorous beetles. We have no evidence of the attacks of any regular enemy, though one usually encounters a certain number of broken shells in each locus. Step (1927, p. 362)

says that in Cornwall sheep have a preference for cliff-pastures where *acuta* and *Helicella virgata* occur, and he seems to have had evidence that the snails are palatable to the sheep. A certain percentage exhibits a curious and significant mark—a hole, about 1 mm. in diameter, drilled through the body-whorl. This may be the exit-hole of a parasite. In some localities a parasitic Dipteran is responsible for a high mortality. Its larvæ may be found living in the bodies

Text-figure 2.



of living and dead snails in large numbers. We have found heavy infections of this form at Burpham (XLVII.) and one colony at Rottingdean (LX.). The life-history of Sarcophagines and their attacks on other Helicoid snails are described by Keilin (1919) and are further alluded to here (p. 1038). The identity of the Sarcophagine that parasitizes *C. acuta* in England has not yet been established. Böttcher (1913, p. 367) states that Giard bred *Sarcophaga setipennis* from *C. acuta*, obtained from near Wimereux.

There is a final point of interest in the bionomics of this form with some bearing on our general problem. In their survey of the post-Pliocene land mollusca of the South of England, Kennard and Woodward (1901, *passim*; Kennard, 1923) cite this species only from Bath (p. 235), Widemouth Bay, near Bude (*l. c.*), and the Cornish Towans (*l. c.*). The first-named deposit is pre-Roman, the second presumably Neolithic, and the Towans are "probably quite modern." The only Pleistocene record is from Newquay (Cornwall) (p. 247), though there is an ambiguous Cornish record of Prestwich's (p. 248) of *Bulimus ventricosus* Drap., which may be an error for *C. acuta*. It is further pertinent to add that in Holocene deposits at Eastbourne, Brighton, and Freshwater there is no trace of it. Its absence is to be noted from Cissbury, St. Catherine's Down (Isle of Wight), Selsey and Dover, places where, had it been plentifully distributed in South England at the dawn of the historic period, one would have expected to find it. One of us (A. E. E.) examined a rich Romano-British deposit at Upper Beeding, not far from Saddlescombe, without finding a trace of *C. acuta*. Although the Holocene and earlier deposits of the South of England are probably not exhaustively known, the survey of Kennard and Woodward is of sufficiently wide scope, and takes in enough of the area in which *C. acuta* is now found, to make it very likely that this species is a newcomer in the south and south-east of England. We would go so far as so to suggest that its arrival in Sussex was subsequent to Roman times. That this form has some means of rapidly spreading seems to be proved by the fact that it is now widely distributed over most parts of Ireland, though in 1862 (Jeffreys, 1862, p. 234) it was said to occur inland only occasionally.

We allude on p. 1039 to the way in which the species seems to get carried about from place to place in Sussex and elsewhere. We are as yet unable to say how this is effected, but Jeffreys (*l. c.* p. 234) has an observation that may throw some light on it. He says that the attachment to grass, etc., is "effected by means of a pellicle secreted in the same way as the epiphragm."

We cannot help thinking that there are some rather exceptional circumstances which govern the local distribution of this species. Thus it is quite well represented on the smaller islands off the Scottish and Irish mainland. Nevertheless, in Stelfox's "Clare Island Survey" it is noted as absent from Clare, Inishturk, and Caher, whereas forms like *Helicella itala* and *Helix aspersa* get on to all the islands. Stelfox (*l. c.* p. 38) comments, with surprise, on its absence from Louisburgh (W. Mayo), an area very rich in snails. Equally surprising to our minds is the fact that, although it has been known since 1841 from the Freshwater Downs in the Isle of Wight, it has never spread eastward of Afton Down in that area.

5. Geographical Distribution of the Patterns.

Before we deal with the intensive study of our Sussex colonies, it will be as well to discuss the distribution of the patterns at large in the British Isles, the Continent, and N. Africa.

We have not undertaken an intensive study of the distribution, as this would involve a critical scrutiny of many doubtful records. As far as we can speak from a general survey the distribution is as follows:—

British Isles (a) *Ireland.* Widely distributed on the coasts and over the central plain (Stelfox, 1911, p. 87).

(b) *Scotland.* North and West Coast. Hebrides. (One East Coast record (dubious).)

(c) *England and Wales.* Coasts, Cumberland south to the Scilly Isles and east from the latter to Peacehaven, Sussex. (Recently occurring at Eastbourne and Ore, near Hastings, but now extinct there.)

DENMARK	Nykjφbing (Westerlund, 1871, p. 109).
SWEDEN	? (Germain, 1908, p. 234).
FRANCE	La Manche and Côtes du Nord south to Biscayan and Mediterranean coasts (Locard, 1882, p. 122). Found inland in certain places where it is permanently established, *e. g.*, Niort (Deux-Sèvres) and Beaulieu (Maine et Loire) (Germain, 1908, p. 234).
SPAIN AND PORTUGAL	South to Gibraltar. In Spain, the central provinces (Hidalgo, 1875, p. 183).
NORTH AFRICA	Morocco and Tunis (Brit. Mus.; Germain (1908)) to Egypt (Connolly (MS.): Pallary (1909)).
CAPE VERDE IS.	Nobre (1909).
ITALY	*Passim* (*cf.* Statuti, 1882, p. 50, etc.).
(?) SWITZERLAND	Romanshorn (Hartmann, 1823, p. 12 (?)) [not in Mermod (1930)].
(?) GERMANY	Freiburg in Breisgau (Hartmann, *l. c.* p. 7) [not in Geyer (1927)].
DALMATIA	Brit. Mus.
"EPIRUS"	Mousson (1859, p. 70).
GREECE	Brit. Mus., etc.
MEDITERRANEAN ISLANDS	*Passim*, E. to Rhodes (Gambetta, 1929, p. 94).
TURKEY	Constantinople (Mousson, 1863, p. 12).
SYRIA	(Mousson, 1854, p. 393).
ARMENIA	Sinope (Mousson, 1863, p 102).

We have obtained a total of 2943 specimens from the whole area (exclusive of the Sussex area), and give in tabular form the distribution of the main pattern types (p. 1031).

	Percentages of A.	B^1.	B^2.
Ireland and Scotland (306)	43·1	38·4	14·9
England, N.W., and Wales (396)	45·2	39·4	15·2
England, S.W. and S. (1523)	31·8	34·3	14·3
France, N.W. and S. (421)	45·1	48·4	6·4
S. Europe and N. Africa (297)	78·4	16·1	5·3

The total number of Sussex specimens from all loci give us the following:—

A.	B^1.	B^2.
33·9	40·8	22·2

Two interesting points are to be made from these figures:—

(1) The Continental series is characterized by its high percentage of class A. As a matter of fact this is due to the remarkably high frequency of the unbanded class (31), which in S. Europe is no less than 56·5 per cent. of the total population. The figures for class 31 are:—

	Percentages.
Ireland and Scotland (2)	Less than 1
England, N.W. and W. (101)	25·4
England, S.W. (260)	17·0
France (43)	10·9
S. Europe and N. Africa (169)	56·5

This increase is made at the expense of class B^2. The South European stock consists, then, of a very low percentage of the "combined" type, the banded and unbanded occurring mainly uncombined.

(2) In Sussex, on the other hand, the reverse process is seen. A touches a very low point and B^1 and B^2 rise at its expense, the increase of B^2 being very marked.

So far as our figures allow us to speak, it seems that the Sussex loci contain a population rather different from the general run of the British and Continental population, and exhibit type-characteristics the reverse of that found in the circum-Mediterranean region.

6. History of the Sussex Colonies.

The history and distribution of the Sussex colonies raise some question of no little interest. It will be as well to give the known facts to begin with.

Area or place.	Date.	Authority.
"Widely distributed . . . between the Adur and Chichester."	1854–1870	Lucas (in Toms).
Sullington, near Storrington	"Many years ago"	Lucas (in Toms, *l. c.*).
Eastbourne (Mill Gap)	1882	Jenner (in Toms, *l. c.*).
Ore	?	Toms (*l. c.*).
Saddlescombe	1917	Robinson (1918).
Rottingdean	1920	Brazenor (in Toms, *l. c.*).
"Along the Rottingdean road as far as Newhaven."	(?) 1926	Toms (MS.).
Saltdean	1926	Ellis (this record).
Burpham.....	1929	Tickner Edwardes (this record).
Amberley	1929	Aubertin and Robson (this record).

At the places mentioned in this list *acuta* is now no longer found at Eastbourne, as the site has been built over. At Ore Mr. A. E. Craven tells us that it is no longer to be found. We believe that there is some evidence that it has been obtained at Lewes, but we cannot confirm the record. We have not been able to get any definite evidence of its occurrence beyond Peacehaven (Portobello), where we took a few stragglers in 1927.

From this record it will be seen that *acuta* seems to have been found inland in several places in Sussex, and now is confined to the coast and places under 6 miles from the latter.

There are two questions which present themselves for solution:—

(1) There seems to be a definite hiatus in the distribution between Dorset and Sussex. The species is found fairly continuously eastwards as far as Lulworth and Winfrith (E. Dorset). But, as far as we can ascertain, the only place in which it occurs between Winfrith and the valley of the Arun is Freshwater and Aston Downs near the Needles, Isle of Wight. We do not assert that it is absent from the intervening area; but having regard to the extent to which the land-snails of the South of England are known, we believe that it would have been recorded before now, had it existed in S. Hampshire, the Selsey area, &c. The county records for this area, however, make no mention of it, and Mr. E. Heron Allen, F.R.S., informs us that it has not been seen in the Selsey Bill area, and the survey made by Miss Palmer, the Hon. L. Lindsey, and Lt.-Col. L. Baker for W. and S. Hampshire and the Chichester area is equally negative. There are three explanations of the apparently discontinuous distribution:—(*a*) It may simply not have obtained a suitable habitat in the area from which it is absent. This is not easy to prove either way. We are inclined to think there are many suitable habitats in S.E. Hampshire, and W. Sussex, *e. g.*, sand-dunes, turfy cliffs, &c., on which it thrives elsewhere. (*b*) It may have been spread into Sussex

by purely accidental means which carried it there and not into Hampshire. This again is speculative. We have a little evidence that it possesses a definite power of adhesion to foreign bodies, and it may have been introduced with West of England cattle. Accidental transport may produce many anomalies of distribution, but it still remains a little curious that S. Hampshire, &c., has not been populated. (c) There remains the possibility that it was once more widely spread and has disappeared from various places in its former area.

(2) This suggestion introduces our second query—Why is the present distribution in Sussex so "patchy"? We believe that it is possible that *C. acuta* may have had a wide distribution in Sussex (Mr. Lucas's records), and owing to the operation of some factor in its environment may have become extinct except in the present patches. The past history of the species in Sussex is surrounded by a slight element of uncertainty. Mr. Jenner, who was a careful collector, only refers to the Eastbourne locus in his Sussex survey (Jenner, 1884). Nevertheless Mr. F. Lucas obtained it between the Adur and Chichester between 1854 and 1870, when he said it was "widely distributed" (Toms, *l. c.*). Thanks to the kindness of Mr. H. Roberts, Director of the Brighton Museum, we have examined some of Mr. Lucas's original W. Sussex forms and can confirm his identification. We believe that Mr. Lucas's record is correct, and that the species was originally plentiful in the area indicated; but it is quite certain that it is not plentiful there now. The only occurrence at the present day is the single colony at Burpham and some stragglers around Amberley (see below). One of us (A. E. E) has intensively studied the mollusc fauna in the Brighton-Lancing-Arundel area without finding it. We therefore believe that its original area of occupation has been diminished in extent, and the question naturally presents itself—What is the cause of this local extinction?

There are two suggestions worth consideration. (1) Mr. J. Wallace Passmore, of Coombes, near Shoreham, who has had much experience of Downland cultivation, has noted that in several places the Downland snail population has been substantially thinned after the introduction of cattle and sheep and of "slagging." The presumed disappearance of *C. acuta* may be the result of recent changes in agricultural practice for which there is some definite evidence. (2) From p. 1034 it will be seen that *C. acuta* is, in parts of Sussex, prone to an infection by a Dipteran parasite which passes its larval stage in the body of the snail with lethal results. The distribution of the parasite is not at all well known, and we do not know how far it can be held to determine the local extinction of *C. acuta*. However, we regard this as a contributory cause of its "patchy" occurrence and of its local disappearance, though not of the major irregularities in distribution alluded to above.

There is, however, a further question, and one very pertinent to our special study. Although we believe the Downs west of Brighton have had their *acuta* population diminished, we are not disposed to accept all the colonies east of Brighton as relict ones. It will be noted (p. 1037) that the Saddlescombe, Rottingdean, and Rottingdean-Peacehaven colonies are all of recent discovery. We are quite ready to believe that the rather remote downland colony at Burpham might have been overlooked by earlier collectors. We cannot believe, however, that the Rottingdean and adjacent colonies could have been missed, as they are in very much frequented country, and some are on a much-used main road. This fact, and their occurrence as isolated colonies very rich in individuals in circumscribed patches, point to the probability that these colonies have been recently founded from individuals accidentally introduced. The Saddlescombe, Saltdean, and W. Rottingdean colonies, as well as the patch above Amberley, are all on roadsides where they could have arisen from individuals dropped from passing vehicles carrying fodder or from the coats of passing cattle or sheep. Actually we have some good evidence of the way in which this species is carried about, as

Mr. G. Rice has recorded that some specimens were taken off the mudguard of a motor-car at Pulborough (1930, p. 26). Further evidence of a very convincing nature as to the very recent establishment of one of our series of colonies is supplied by Miss Maud Robinson who originally discovered (1917) the Saddlescombe colony. She said in her published account (1918, p. 38) that the species "had never come under my notice before [1917]." She now informs us that she and the members of her family had been for a long time careful observers of the fauna of the Downs around Saddlescombe, and that for many years she had collected the land-snails of this district without observing *C. acuta*. The species was actually known to her, as she had received it from Somerset. Nevertheless, it was not until 1917 that the colony on the Saddlescombe-Brighton road was noticed. Actually the colony was traced to its headquarters from a single specimen that was brought into Miss Robinson's house on a basket that had been kept on the bank which is now so thickly populated—a further testimony of the way in which *C. acuta* is transported from place to place.

We think that Germain's account of sporadic and short-lived colonies that have been found inland in France (1908, p. 234) is further evidence on this point. In short, although the Sussex population may be in general an old one, we believe that the colonies east of Brighton are of quite recent origin, probably not more than 15–16 years old, and in some cases less.

This has a very important bearing on the question of colonial divergence. If the colonies, *e. g.*, at Saddlescombe and Saltdean, are composed of recent wanderers from a focus at Rottingdean, or *vice versâ*, it should be noted that significant deviations have manifested themselves already in the isolated sections. We do not say that the relationship between the colonies which we have sketched is proved. All that we wish at present to suggest is that the Brighton group is not composed of long-established colonies in which the divergence has been slow.

7. Description of the Habitats of the Sussex Colonies.

The following list gives (*a*) the register number of each colony; (*b*) the description of the habitat; (*c*) the associated mollusca; (*d*) the associated plants; and (*e*) the pH value of the soil*. The exact position of the stations is indicated on the map (p. 1030):—

1. (*a*) D.C.R. (Rottingdean, Dean's Court Road).
 (*b*) Low wide bank, almost horizontal, no top drainage; very chalky soil.
 (*c*) *Trichia striolata*, *T. hispida*, *Helicella virgata*, *H. gigaxii*, *Helix aspersa*, *Oxychilus cellarius*, *Agriolimax agrestis*.
 (*d*) *Plantago lanceolata*, *P. major*, *Matricaria inodora*, *Potentilla anserina*, *Galium mollugo*, *Festuca ovina*, *Dactylis glomerata*, *Rumex acetosa*, *Achillea millefolium*.
 (*e*) pH 7·5.

2. (*a*) XXV. (Saltdean).
 (*b*) Steep bank, about 20 yards from the sea and 15 feet above it; mainly rough chalk rubble; about 70 degrees slope off main road; top drainage.
 (*c*) *Helix aspersa*, *Cepæa nemoralis*, *Trichia hispida*, *Helicella virgata*, *H. caperata*, *Agriolimax agrestis*.

* The pH value was taken in the field with a B.D.H. soil-testing outfit and afterwards checked by laboratory tests kindly carried out by Mr. M. Hey (Mineralogical Dept., British Museum).

(*d*) ***Potentilla anserina***, *Centaurea nigra*, *C. scabiosa*, *Hieracium* ***pilosella***, ***Festuca ovina***, ***Plantago lanceolata***, ***Reseda lutea***, ***Achillea millefolium***, ***Cnicus arvensis***, ***C. lanceolatus***, ***Leontodon autumnale***, ***Convolvulus arvensis***.

(*e*) pH 7·5.

3. (*a*) XXIX. (Saddlescombe).

(*b*) High bank, about 10 feet high and 45 degrees slope, with upper drainage.

(*c*) ***Trichia striolata***, ***Theba cantiana***, ***Oxychilus cellarius***, ***Helix aspersa***, ***Helicella gigaxii***.

(*d*) ***Avena pubescens***, ***Urtica dioica***, ***Cnicus lanceolatus***, ***Carduus crispus***, ***C. nutans***, ***Sonchus asper***, ***Galeopsis tetrahit***, ***Galium mollugo***, ***Pimpinella saxifraga***, ***Arrhenatherum elatius***, ***Rumex crispus***, ***Anthriscus sylvestris***, ***Silene cucubalus***, ***Lychnis alba***, ***Stachys ambigua***, ***Potentilla reptans***, ***Heracleum sphondylium***, ***Brassica arvensis***, ***Daucus carota***, ***Festuca ovina***, ***Dactylis glomerata***, ***Plantago lanceolata***, ***Centaurea scabiosa***, ***Poterium sanguisorba***, ***Convolvulus arvensis***, ***Lapsana communis***.

(*e*) pH 7·5.

4. (*a*) XXX. (Saddlescombe).

(*b*) High bank, 12 feet high, about 30 to 40 degrees slope; upper drainage.

(*c*) ***Oxychilus cellarius***, ***O. alliarium***, ***Helicella virgata***, ***H. caperata***, ***Theba cantiana***, ***Helix aspersa***, ***Trichia striolata***.

(*d*) ***Achillea millefolium***, ***Ononis repens***, ***Hypericum perforatum***, ***Centaurea scabiosa***, ***Phyteuma orbiculare***, ***Galium verum***, ***Vicia cracca***, ***Veronica chamædrys***, ***Urtica dioica***, ***Heracleum sphondylium***, ***Avena pubescens***, ***Phleum pratense***, ***Festuca ovina***, ***F. pratensis***, ***Pimpinella saxifraga***, ***Poterium sanguisorba***, ***Scabiosa succisa***, ***Picris hieracioides***, ***Hypochœris radicata***, ***Plantago lanceolata***.

(*e*) pH 7·5.

Remarks.—XXIX. and XXX. are separated by about 30 yards of brambles, in which *Cochlicella acuta* is absent.

5. (*a*) XXXI. (Saddlescombe).

(*b*) Low bank, 3 feet high, no top drainage, 25 to 30 degrees slope; much plant débris on top.

(*c*) ***Helicella gigaxii***, ***H. virgata***, ***Helix aspersa***, ***Theba cantiana***, ***Trichia striolata***.

(*d*) ***Urtica dioica***, ***Dactylis glomerata***, ***Arrhenathrum elatius***, ***Centaurea scabiosa***, ***Convolvulus arvensis***, ***Anthriscus sylvestris***, ***Silene cucubalus***, ***Avena pubescens***, ***Potentilla reptans***, *P anserina*, ***Rumex obtusifolius***, ***Scabiosa arvensis***, ***Carduus crispus***, ***Heracleum sphondylium***, ***Bromus sterilis***, ***Agropyron repens***.

(*e*) pH. $>7·0$, $<7·5$.

6. (*a*) XXXII. (Saddlescombe).

(*b*) Low bank, 3 to 4 feet high, no top drainage, 30 degrees slope; a good deal of old hedge-débris on top.

(*c*) *Trichia striolata, Helicella virgata, H. gigaxii, Helix aspersa.*

(*d*) *Veronica chamædrys, Potentilla reptans, Festuca ovina, Dactylis glomerata, Convolvulus arvensis, Lotus corniculatus, Centaurea scabiosa, Plantago lanceolata, Ononis repens, Achillea millefolium, Avena pubescens, Urtica dioica, Arrhenatherum elatius, Galium mollugo, Anthriscus sylvestris.*

(*e*) pH 7·0.

Remarks.—Trimmed in 1929; many dead shells, living specimens scarce.

7. (*a*) LX. (Rottingdean, W.).

(*b*) Low bank by main road, near edge of cliff. *Cochlicella acuta* plentiful over an area of about 30 square yards.

(*c*) *Helicella virgata, H. caperata, Helix aspersa, Trichia hispida, T. striolata.*

(*d*) *Senecio vulgaris* (abundant seedlings), *Plantago coronopus, Cnicus lanceolatus, Lepidium draba, Malva rotundifolia, Festuca ovina, Dactylis glomerata, Achillea millefolium.*

(*e*) pH $>7\cdot5$, $<8\cdot0$.

8. (*a*) LXI. (Rottingdean, W.).

(*b*) Steep bank on north side of main road, a little further from the sea and nearer to the village than LX.

(*c*) *Trichia hispida, Helix aspersa, Helicella virgata, H. caperata, Oxychilus cellarius.*

(*d*) *Picris echioides* (snails very abundant on this plant), *Senecio vulgaris* (seedlings), *Achillea millefolium, Malva sylvestris, Dactylis glomerata, Lycium chinense, Festuca ovina, Convolvulus arvensis, Taraxacum vulgare, Poa annua.*

(*e*) pH 7·5.

9. (*a*) XLVII. (Burpham).

(*b*) Field-surface (fallow, regressing to grass after plough) and adjacent banks.

(*c*) *Theba cantiana, Helicella caperata, H. gigaxii, H. virgata.*

(*d*) *Rumex crispus, Plantago lanceolata, Trifolium repens, Galium aparine, Linum catharticum, Senecio vulgaris, Ranunculus repens, Anagallis arvensis, Medicago lupulina, Agrostis alba, Dactylis glomerata, Sonchus asper, Cnicus arvensis, C. lanceolatus, Polygonum aviculare, Viola arvensis.*

(*e*) pH 7·5.

8. Analysis of the Sussex Colonies.

After the pattern of each individual shell had been determined (p. 1030), the percentages of the three main types (A, B^1, and B^2) were calculated for each colony and for each year in which collections were made. These results are tabulated on p. 1042. It thus becomes possible as a preliminary to see how the percentage of a given character varies from year to year and from colony to

colony. It is evident that such differences as occur cannot be taken at their face-value until the sources of statistical error have been eliminated. This has been done by subjecting them to the normal test for "significance," for the explanation of which we are indebted to Dr. E. M. Elderton.

TABLE I.

	Year.	Specimens examined.	A.	B^1.	B^2.
D.C.R.	1920	(183)	60·1	20·2	19·6
	1922	(202)	56·1	23·5	20·2
	1927	(165)	53·3	20·6	22·4
	1928	(175)	54·2	23 4	21·4
XXV.	1928	(169)	50·2	25·4	21·8
	1929	(165)	50·9	14·5	32·1
LX.	1929	(165)	43·0	23·0	29·1
LXI.	1929	(191)	60·7	14·1	25·1
"Saddlescombe"	1925	(209)	38·2	36·3	25·3
XXIX.	1928	(170)	37.0	39·4	20·5
	1929	(170)	28·8	44·7	20·0
XXX.	1927	(166)	31·3	38·5	27·1
	1928	(170)	25·2	54·1	15·8
	1929	(150)	28·6	54·6	14·0
XXXI.	1927	(166)	22·8	51·8	22·8
	1928	(161)	23·6	63·3	11·8
	1929	(72)	22·2	51·3	23·6
XXXII.	1927	(170)	22·9	51·7	22·3
	1928	(169)	26·6	53·4	19·5
	1929	(170)	27·6	52·9	17·1
XLVII.	1929	(170)	31·1	34·1	31·7

The procedure is as follows. If the percentage of a given character in one colony (A) be x, and in another colony (B) y, it is required to show whether $x-y$ is significant.

Colony A: $$\frac{\sqrt{x(100-x)}}{\sqrt{\text{number of individuals}}} = E_1.$$

Colony B: $$\frac{\sqrt{y(100-y)}}{\sqrt{\text{number of individuals}}} = E_2.$$

Then $\sqrt{E_1^2+E_2^2}$ = standard error of difference $x-y$ (s. d.).

If $x-y$ = s. d. $\times 3$, the difference is significant.

If $x-y$ = s. d. $\times 2$ „ „ „ probably significant.

If $x-y <$ s. d. $\times 2$ „ „ „ not significant

We have allowed ourselves, in tabulating our comparisons, to treat certain differences as "very probably" or "possibly" significant, according to the degree to which the figures involved approximate to the standards given above.

The results of these tests for significance are given in full in Table III.

Interpretation of results.

(*a*) An examination of the data in Section 7 has convinced us that the characters under consideration are not influenced by the particular environments in which the animals live, and are of a fixed heredity. As far as the main "flammulate" and banded pattern and certain band-phases are concerned, we are indebted to experimental evidence kindly supplied by Mr. Hugh Watson, who conducted breeding experiments with *C. acuta*, the results of which are as yet unpublished. It seems that the characters just mentioned are hereditary, and exhibit simple Mendelian behaviour.

In addition, we have examined the flora and fauna associated with each colony, the pH value of the soil of the habitats and the general nature of the latter (especially as far as edaphic conditions are concerned). Finally, we have examined a large series of forms from a great diversity of loci of different climatic and geological nature. In general we are inclined to think that one character (the extent to which a melanic condition is assumed) is largely determined by environmental conditions.

Nevertheless, neither in our intensive survey of the Sussex loci nor in the wider geographical survey can we find any suggestion that the three characters investigated in this study occur in particular habitats or are causally associated with any particular environmental conditions.

Some detailed observations should make this clear. In general colonies D.C.R. and XXV. have very similar populations, yet the habitats are markedly different in general character. On the other hand the habitats of LX. and LXI. are quite similar in character, and yet their populations differ. The habitat of the Burpham colony (XLVII.) is totally unlike the Saddlescombe and Rottingdean groups, and yet XLVII. has much in common with the former in quality of the population. The question of pH value of the soil in the various habitats scarcely seems to arise, as the various soils differ scarcely at all, and we find pattern-differences associated with similarity of pH value. Again, the differences in vegetation observed between the various habitats are not, according to Mr. A. J. Wilmot, of any ecological importance, as they do not depend on differences of soil, etc. It is, indeed, open to the hypercritical to object that, because *Rumex acetosa* is present in colony D.C.R. and absent in XXIX., the significant differences in pattern may be associated with this difference in the plants. But it is then necessary to inquire how it is that, though this plant is absent in XXV. and present in D.C.R., the snails from this pair of colonies are alike. Lastly, we should point out that all our colonies are obtained from chalk pasture-land within 5 miles of the sea, and, as far as the meagre records go, with a more or less similar rainfall.

A few instances from our geographical series should endorse these conclusions. The Hon. Anne Palmer obtained for us a large series from dune-pasture at Paignton (Devon), a habitat which in all essentials resembled a similar locus at St. Mary (Scilly Is.). Yet the Paignton series had 92 per cent. of the non-banded white type (31) and the Scilly series had none at all!

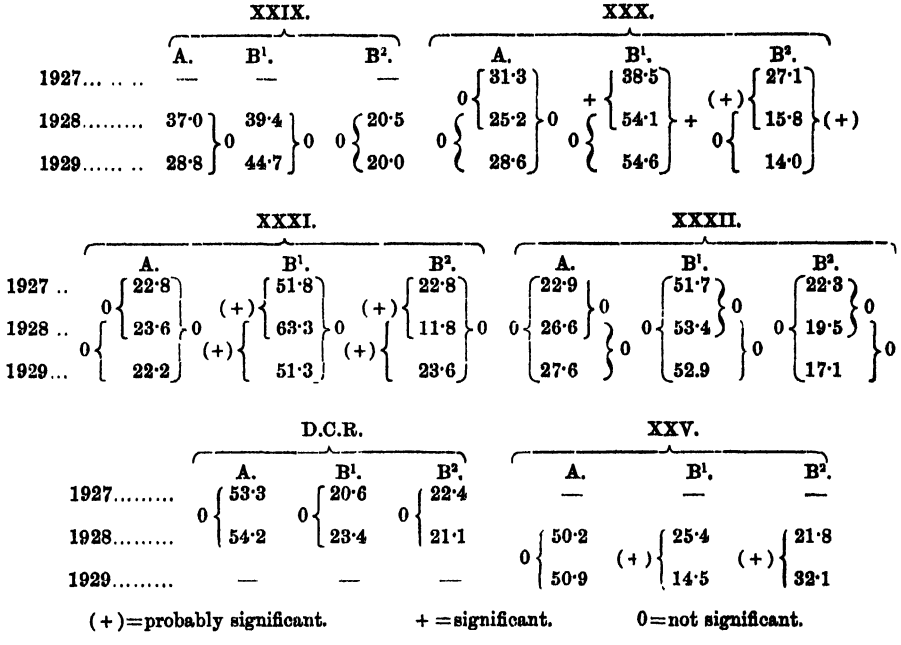
Again, we find that over all the European and N. African area the proportion of the banded type (B^1) remains remarkably constant, and is quite unaffected by climatic conditions.

We do not claim that the entire range of environmental factors has been explored. But we feel that if the effect of climate and rainfall, distance from the sea (which involves the amount of spray-borne chlorine deposited on the land-surface), associated plants, the general character of the habitat, and the pH values of the soil can be excluded, that there is very little else that can be suspected of influencing the colour-pattern.

(*b*) The extent to which the pattern in the various colonies remains constant from year to year may be estimated from Table II.

Table II.

Showing Annual Changes in Pattern-class in Colonies of *C. acuta*.



We give there the percentages of our three classes in colonies XXIX., XXX., XXXI., XXXII., D.C.R., and XXV. for two years (three colonies) and three years (three colonies). If the percentage of each character in each year be compared with those of other years in the same colony, it will be seen that there are 36 possible comparisons. The differences in all these 36 cases have been subjected to the test for significance described on p. 1042, with the following results:—

26 comparisons (72·2 per cent.) show no significant difference.
8 „ (22·2 per cent.) show probably significant difference.
2 „ (5·5 per cent.) show significant difference.

On the whole these figures show that the colonies have remained tolerably constant over the period of observation.

A further confirmation of this impression is gained if the figures for colony D.C.R. (Table I.) are studied. This colony remained constant in all three characters for the eight years 1920–1928.

We must point out that three out of the six colonies remain entirely constant over the period of examination. Of the others, one (XXX.) remains unaltered in one character (A), changes in the two other characters (B^1 and B^2) at the second year, and remains constant to that change for the third. Colony XXXI. remains constant in A, changes in B^1 and B^2, but reverts to the original percentages in the third year. XXV. was only examined for two years in which A was constant and B^1 and B^2 again changed. It is curious to note that it is B^1 and B^2 that are unstable in all three cases. This result may be compared with the similar result observed by Boycott (p. 1049) in *Clausilia*.

Of course it is impossible to say how far the character of the various colonies will be maintained over a longer term of years. Those which are found to be entirely constant for the shorter terms of two to three years (XXIX. and XXXII.) may even manifest change at the fourth or fifth year. In general, however, the impression conveyed is that of a considerable measure of stability. Half the colonies remain unchanged in all their characters, and 72·2 per cent. of the comparisons of single characters show that no change took place. The general bearing of this result is discussed on p. 1047.

(*c*) *Size differences.*—In addition to the elimination of errors that might arise from sampling, and to the evaluation of the effect of environment and annual change, there are certain other sources of error that it is customary to consider in making statistical comparisons of the kind used in this paper. The question of sexual differences naturally need not be considered in a monœcious form such as *C. acuta*. The extent to which age-differences between the members of different colonies might vitiate our comparison must, however, be seriously considered. Could it be shown, for example, that there were patterns more characteristic of the earlier stages of growth than of the later, then a colony of young specimens might show percentages of the patterns different from a colony of older specimens.

After examination of the various growth-stages it has become quite evident that neither of the pattern-elements which are singly and in conjunction considered here is liable to such modification with growth as might vitiate our conclusions. (*a*) *The flammulate pattern* is manifested very early in development, and is clearly seen on the third whorl and onwards. Occasionally late development of the flammulæ is observed, and once or twice we have seen some cases of cessation of the flammulate type. There is some loss of intensity in the pigmentation of the apical whorls, so that in very large shells the body-whorl is darker than, *e. g.*, whorls 1–5. None of these facts, however, alters the conclusion that, as the pattern is developed early and persists into the adult stage, the pattern of shells of 11-12 mm. is in exactly the same condition as those of 17 mm. (*b*) *The banded types.*—The band makes its appearance very early in development. Some trace of pigment is seen in the second whorl, and at about the fourth it is well developed. Shells of 3–4 mm. therefore show the band quite as definitely as older ones. Anomalies of band-development occur; but, as the bands normally appear at an early stage and are not liable to any frequent disturbance, it is highly improbable that, because a shell is 5 mm. smaller than another, any significant differences as between bandedness and non-bandedness will be involved. In fact, we hold that the effect of size-differences may be definitely ruled out of consideration.

(d) *Intercolonial Differences.*—There are three points for discussion here: first, to what extent do the colonies tend to exhibit "significant" differences; second, what is the origin of these differences; and third, have they any interest and importance for the general problem of local divergence and evolution?

1. The first question is readily answered by the data at the foot of Table III. Ignoring the cases of "possible" and "probable" significance, we find that, of a total of 147 comparisons of the single characters, there were

54 significant differences (36·2 per cent.).
63 non-significant differences (42·8 per cent.).

Speaking generally, we may say that the colonies show about as much significant divergence as non-significant.

2. It is not easy to decide what the origin of the annual and intercolonial differences may be. We have shown (p. 1043 and following) that within the limits of the available ecological data there is no evidence that they are due to the direct effect of the environment. It is possible that some selective process may be at work;

TABLE III.

Showing Comparisons of all Colonies over Three Years.

	1927.			1928.			1929.		
	A.	B^1.	B^2.	A.	B^1.	B^2.	A.	B^1.	B.
D.C.R./XXV.	—	—	—	0	0	0	—	—	—
D.C.R./LX.	—	—	—	—	—	—	—	—	—
D.C.R./XXIX.	—	—	—	+	(+)	0	—	—	—
D.C.R./XXX.	+	+	0	+	+	0	—	—	—
D.C.R./XXXI.	+	+	0	+	+	(+)	—	—	—
D.C.R./XXXII.	+	+	0	+	+	0	—	—	—
D.C.R./XLVII.	—	—	—	—	—	—	—	—	—
XXV./LX.	—	—	—	—	—	—	0	(+)	0
XXV./XXIX.	—	—	—	(0)	(0)	0	+	+	(+)
XXV./XXX.	-	—	—	+	+	0	+	+	+
XXV./XXXI.	—	—	—	+	+	(+)	+	+	0
XXXV./XXII.	—	—	—	+	+	0	+	+	+
XXV./XLVII.	—	—	—	—	—	—	+	+	0
LX./XXIX.	—	—	—	—	—	—	(+)	+	(0)
LX./XXX.	—	—	—	—	—	—	(+)	+	(+)
LX./XXXI.	—	—	—	—	—	—	+	+	0
LX./XXXII.	—	—	—	—	—	—	(+)	+	(+)
LX./XLVII.	—	—	—	—	—	—	(0)	(0)	0
XXIX./XXX.	—	—	—	(0)	+	0	0	0	0
XXIX./XXXI.	—	—	—	0	+	(0)	0	0	0
XXIX./XXXII.	—	—	—	(0)	(+)	0	0	0	0
XXIX./XLVII.	—	—	—	—	—	—	0	(0)	(0)
XXX./XXXI.	0	(+)	0	0	0	0	0	0	(0)
XXX./XXXII.	0	(+)	0	0	0	0	0	0	0
XXX./XLVII.	—	—	—	—	—	—	0	+	+
XXXI./XXXII.	0	0	0	0	(0)	(0)	0	0	0
XXXI./XLVII.	—	—	—	—	—	—	(0)	+	(0)
XXXII./XLVII.	—	—	—	—	—	—	0	+	+
LXI /LX.	—	—	—	-	—	—	+	(+)	0
LXI./D.C.R.	—	—	—	—	—	—	—	—	—
LXI./XXV.	—	—	—	—	—	—	(+)	0	0
LXI./XXIX.	—	—	—	—	—	—	+	+	0
LXI./XXX.	—	—	—	—	—	—	+	+	0
LXI/XXXI	—	—	—	—	—	—	+	+	0
LXI/XXXII.	—	—	—	—	—	—	+	+	0
LXI./XLVII.	—	—	—	—	—	—	+	+	0
	18 Comparisons.			45 Comparisons.			84 Comparisons.		
	Significant, 6.			Significant, 15.			Significant, 33.		
	Not significant, 10.			Not significant, 19.			Not significant, 34.		
	Probably significant, 2.			Probably significant, 4.			Probably significant, 9.		
				Possibly significant, 7.			Possibly significant, 8.		

Explanation of symbols as in Table II.
(0)=possibly significant.

but as far as the conditions of life in the various colonies are known, this does not seem likely. We do not, however, feel justified in setting this possibility aside until the figures have been analyzed and the subject reviewed by a biometrical

expert. In general it seems to us likely that the differences in question are due to causes in which the environment, either directly or indirectly, has no part. The fact that there is a considerable amount of local divergence, the significant differences in the percentages of the various characters being distributed at random, and with no apparent relation to environmental differences, seems to suggest that the differences are due to the sorting-out in localized and isolated communities of original genotypic divergences present in the older population from which the colonies were originally (p. 1038) derived. The divergences noted here might well have arisen simply because the colonies were formed at the offset by individuals which differed in each instance in genotypic constitution. If this supposition is correct it is not without interest to speculate whether the chance that the new colonies would be founded by individuals differing in their hereditary constitution was favoured at the offset by differences in the percentage-incidence of the characters in the parts of the original population from which such individuals were abstracted. We believe, however, that if the colonies were originally formed not from a few individuals, but from many, it would be more likely that a single colony would reproduce the particular facies of that part of the original population from which it was derived. On the whole, the evidence given on pp. 1038–1039 suggests that the colonies are formed from single or a very few individuals rather than from large numbers. We would like to point to an interesting fact that has some bearing on the question as to whether local variation in percentage-incidence of characters within a population has any effect on the constitution of colonies or communities derived from it. In the one area in which a long stretch of contiguous colonies has been examined, viz., the ¼ mile of bank that includes XXIX., XXX., XXXI., and XXXII. at Saddlescombe, there are no significant differences in the colonies either at the opposite ends or between those in the middle and at the end.

Attention may be also drawn to another important fact revealed by this study. On the whole, the distance between the isolated colonies seems to bear little relationship to the degree of intercolonial divergence. The colonies at Saddlescombe, which are all quite adjacent, show, it is true, very little difference *inter se*. The same is true of the tolerably close colonies at D.C.R. and XXV., though here there is more divergence. But LX. and LXI., which are quite close to one another, show considerable difference, and the remote Burpham colony (XLVII.) does not differ from the Rottingdean and Saddlescombe groups as much as one would expect.

3. The amount of annual change in the constitution of our colonies makes us very unwilling to hazard any suggestion as to the general significance of the divergences described here. It is true (p. 1044) that the degree of constancy exhibited is very considerable. We do not think, however, that the annual deviations can be ignored, and they render the constitution of any colony over a long term of years a highly questionable matter. The most that we feel entitled to say is that processes leading to local differentiation seem to be at work, and that, if sustained in some fair measure, they may be contributory to more marked divergence.

Closely-allied races and species sometimes differ in the percentage-incidence of character-classes, and not qualitatively alone. Such differences as are revealed by this study, if maintained and amplified, might be the basis of major divergences. How the amplification of such divergences would be achieved (*e.g.*, whether it could proceed unaided by selection) is naturally an open question. But it is permissible to suggest that the slow local sorting-out and isolation of diverse elements differing in the percentage-incidence of character-classes may sometimes be an important preliminary to more marked and sustained divergence.

Previous Work.—Intensive analysis of variation in and between separate colonies of land-snails has been undertaken by Crampton (1916, 1925), Boycott

(1919, 1927), Aubertin (1927), and Alkins (1928). So far as they are relevant to our inquiry, the results of this earlier work may be summarized as follows:—(1) Aubertin worked on colonies of *Cepæa hortensis* and *nemoralis* obtained in Wiltshire (four colonies), Suffolk (one), Cornwall (one), Devon (one), Dorset (two), and Middlesex (one). Her scheme of work is analogous to our own, as the Wiltshire group occupies a compact series of adjacent loci varying from ¼ mile to 20 to 30 yards apart, and the rest form a series of progressive remoteness from the Wiltshire group. Aubertin (*l. c.* p. 561) gives percentages of various types of ground-colour and banding. Her series of individuals from each locus are small (30-56), as they were not primarily intended for work of this order, but for anatomical study. However, they are reasonably near the quantity recognized as desirable for such a study, and her results, if not of fundamental importance, are of interest.

We have worked out the statistical value of Aubertin's percentages with the following results:—

(a) *C. hortensis.*

Four adjacent (Wiltshire) and one remote colony (Bucks) were studied. For ground-colour the adjacent colonies show a high percentage of "probably significant differences" in two characters. Two comparisons are "significant" and two are not. The other two characters both yield non-significant differences. The Buckinghamshire colony resembles in general one of the Wilts colonies (H), though "pink" is absent in the latter and has an 8·4 per cent. representation at Iver.

In banding, the comparisons yield two "probably significant" comparisons, two "possibly" and two "not significant" for one character, and more or less the same condition appears in others. On the whole there is a fairly marked amount of divergence judged by *single characters.*

(b) *C. nemoralis.*

The five remote colonies (Cornwall, Middlesex, Devon, Dorset, and Suffolk) were dealt with here. The differences and resemblances are chaotic, and have no relation to distance apart. For example, in colour the Cornish and Middlesex colonies are relatively similar, and they are more like the Devonshire one than the Dorset. In banding, the Suffolk colony is like that from Devon as a whole. In the percentage of single characters the Suffolk, Dorset, and Devon colonies agree in one, the Cornish and Middlesex colonies in another, and so on.

Broadly speaking, the result of this survey is to suggest that, though adjacent colonies may sometimes differ in individual characters in a way which is statistically significant or probably so, such differences are not in any way related to the degree of separation. The degree of difference and resemblance in total facies, though more difficult to assess, seems also to be independent of the amount of distance between the colonies.

Boycott (1919, 1927) studied the proportions of the shell of ten colonies of *Clausilia rugosa* collected in the neighbourhood of Portmadoc (Carnarvonshire). We are here dealing with observations on a different kind of character, viz., the shape of the shell. The work is of value for comparison, however, and, in addition, is important, as Boycott, like ourselves, studied the same colonies at different periods, in this case the interval being ten years. His results may be briefly summarized as follows:—

Two characters—altitude and diameter—were studied. The comparison of altitude gives in six pairs of adjacent colonies (A × B, C × D, E × F, E × G, F × G, H × I), five significant differences, and one not significant. For diameter, curiously enough, the case is different, four differences being non-significant and two being significant. Boycott finds that "in general the characteristic size for each locus is maintained," while "the 1924 (later series)

are generally narrower" (1927, p. 134), the difference being significant in all cases but one (p. 133). He points out (*l. c.*), however, that "the relative positions of the different loci in the series remain substantially the same."

The comparison of remoter loci gives significant and non-significant differences apparently irrespective of the amount of distance between the colonies. There are 25 out of 39 possible comparisons significant differences in altitude, and 17 out of 39 in diameter.

The interesting points in Boycott's papers are (1) the general agreement with Aubertin's results in so far as the lack of correlation between degree of divergence and distance apart of the colonies; (2) the change in diameter; (3) the difference in amount of divergence between altitude and diameter; and (4) the constancy in size over ten years. Boycott (1919, p. 21) evidently suspects some relationship between altitude of the shell and the nature of the habitat.

3. Alkin's work (1928) deals with two species of *Clausilia*, *rugosa* and *cravenensis*, obtained from 19 loci round the Kent estuary (Lancashire), the area covered by these being about 8 × 4 miles. Two characters were studied—altitude and major diameter. His excellently-presented results are not arranged in such a way as to make them comparable with ours. We may, however, extract the following conclusions from his summary, which are in accordance with our results:—(1) In general, series from neighbouring loci are much alike, but the converse is not true; (2) "it has not been possible to correlate the characters of the shells with the characteristics of their loci."

4. Crampton's work is on a much larger scale than any of the preceding studies. It embodies the result of many years' study of the genus *Partula* in the islands of Tahiti, Guam, and Saipan, and it is quite impossible to summarize it in this work. The size, shape, and colour-pattern of many species are dealt with, and the results are not presented in such a way as to make their significance readily perceptible without an elaborate analysis. One of us has, however, undertaken this in a limited section of the data relating to colour-pattern. From the study of *P. otaheitana* on Tahiti the following facts may be deduced:—

(1) The same percentages of given classes may be found in remote loci.
(2) Colonies in adjacent loci *tend* to be alike; but
(3) marked change may occur between adjacent loci, *e.g.*, between Ururoa and Tuauru (1925).
(4) Adjacent colonies may differ in the absence or presence of whole colour-classes.
(5) Environment has nothing do to with the percentage-incidence of the various colour-classes.

We do not claim that this example of Professor Crampton's results is representative of the whole, though we suspect that it may be so.

We believe that the general results of these studies show that, while adjacent colonies or series tend to be alike (Boycott's results on the altitude of *Clausilia* being a marked departure from this rule), there is very little relationship between the amount of distance between colonies and the degree of structural divergence found in the latter. In the characters studied, environment may have something to do with shell-shape (Boycott), but there is no suggestion that pattern is so affected. The random development of genetic differences in the constitution of colonies at their inauguration seems to be the chief agency at work.

9. The Problem of Melanism in *C. acuta*.

In collecting the data discussed in the previous sections we have encountered some facts of considerable interest which call for separate treatment. It soon

became impressed on our notice that there is a high percentage of dark forms in many loci in the West of England and in Ireland, and we took steps to collect as much data on this subject as we could.

A melanic pattern in *C. acuta* seems to arise in two main ways. (1) The dark area between the flammulæ in types A and B^2 and their derivatives becomes intense and spreads at the expense of the flammulæ until the whole of the last whorl is black or deep chocolate. (2) The two bands of type B^1 and its derivatives coalesce and extend upwards until a similar condition to (1) is found.

We give below, in tabular form, the percentage of these melanic forms in the four main areas.

Scotland and Ireland 67,	= 21·8	per cent.
England, N.W. and Wales, 213	= 53·8	,,
,, S.W. and W., 389	= 30·7	,,
Channel Is. and N. France, 95	= 26·1	,,
S. Europe and N. Africa, 22	= 5·5	,,

There seems to be no notice in literature of the occurrence of dark forms of *C. acuta* from north-western or insular stations, but Dupuy (1839, p. 313) records "*B. maritimus*" (a form of *acuta* from La Rochelle) "d'un brun vert fort remarquable."

It will be seen that the N.W. littoral of Europe is occupied by a population with a very high percentage of melanic forms that attains its maximum in N.W. England (including the Isle of Man) and Wales. About these facts we do not think there is much doubt. As to the interpretation, we feel that this will not emerge until the question of the cause of melanism has been fully explored. In the meantime we offer the following observations.

Melanism in animals has been said to be due to various environmental factors, *e. g.*, humid atmosphere, extremes of temperature, strong light, and certain metallic salts. The action of the climatic factor has been claimed in Birds and Mammals ('Gloger's Law,' Rensch, 1929, p. 152). The effect of salts is well known from the observations of Harrison (1920) and the experiments of the latter and Garrett (1926, p. 241) Some stress has been laid on the frequency of melanic forms in small islands (Mollusca (Rensch, 1928, p. 1; Sturany, 1902, p. 381), Lizards (Boulenger, 1913; Mertens, 1924; Kammerer, 1926)). "Insular melanism," it has been suggested, may in certain instances be due to the special humidity of insular habitats. Kammerer (*l. c.*) believes that the strong sunlight, heat, etc., characteristic of some of the Dalmatian Islands, are responsible for the melanism of the Lizards found thereon. This view is criticized by Mertens (*l. c.* p. 47, and following). Eisentraut (in Rensch (1929, p. 179)) makes the interesting observation that in the Balearic Is. the melanic lizards feed on Halophyta in the absence of insects, and suggests that the melanic condition is due to the salts contained in the plants. Harrison (1920, p. 245) thinks the littoral and insular melanism observed in Lepidoptera in the Hebrides may be due to spray-borne salts.

The causes of melanism are plainly multiple, and the various groups of animals seem to respond in a different way to different pigment-controlling factors. In the land Mollusca the general rule seems to be that "qu'en général, tandis que la chaleur provoque la formation du pigment, le froid détermine sa diminution ou même sa disparition complete" (Germain, 1928, p. 134). Nevertheless low temperature also seems to produce darkening sometimes. Humidity is assumed to act, as in Birds, as a stimulus to darker pigmentation (Germain, *l. c.* pp. 135, 138; Mandoul, 1903, p. 382). This view rests on geographical data (*e. g.*, the fact that the individuals of given species in a humid climate are darker than those in a drier country), and we know no experimental data on the effect of humidity on Molluscs. How capricious the occurrence of melanic forms is

v. below), and how hard it is to associate it with any external factor, may be seen in Dean's (1923) account of the Mollusca of South Wales. He says (p. 58): "In South Wales there is a general tendency in snails, as in insects, towards melanism. Dark forms of *Helix aspersa*, *nemoralis* and *hortensis* predominate. Brown forms of *Helicella virgata* and *caperata* may be passed over for *Hygromia*." Nevertheless we find (*l. c.*) that "*Helix hortensis arenicola*, in which the band-pigment is absent, occurs abundantly all over Monmouthshire and Glamorgan." *Helix aspersa* var. *exalbida* occurs all along the same coast. White examples of *Theba cantiana* often outnumber the type.

At first sight it seems as though the climatic factor might be successfully invoked to explain the occurrence of darker forms of *C. acuta* down the western littoral of Europe. The area in which melanism attains its maximum, viz, N.W. England, the Isle of Man, and Wales, is one which has a very heavy rainfall; that in which it is at a minimum, viz., N. Africa, has a very low one. As soon, however, as we look at the facts more closely we are disinclined to accept this explanation. The Scilly Isles have a high percentage of melanics, but they have a relatively low rainfall (31–32 in. annually). Sussex generally has about the same (25–36 in.), and yet it is singularly deficient in melanics. We have had no melanics from Torquay and Paignton (about 33 in.), but many from Weymouth (27–28 in.). Two marked centres of melanism (Tenby (40·9 in.), and the Isle of Man (41–43·9 in.)), are areas with a rather high rainfall, but the Channel Isles, which are equally rich in melanics, have no record of rainfall higher than 33·2 in. It is just possible that these anomalies might be explained by more intensive collecting and ampler data; but we do not think it likely. It might be argued that, although Scilly, Weymouth, and other places with numerous melanics have a low rainfall for the British Isles, yet it is high when compared with that of the Mediterranean generally. Nevertheless Sussex, by a similar token, should be reckoned as having a high rainfall, but it is definitely poor in melanic forms. On the whole, then, we are forced to admit that humidity is not likely to be the chief agency in producing melanism in *C. acuta*.

Harrison's suggestion that spray-borne salts are responsible is also tempting at first sight. Many of the stations from which melanics are obtained are exposed to strong winds which must carry spray in liberal doses over the dunes, etc., on which the snails live. On the other hand, we have many series from similarly exposed loci that show no melanism at all. There can be little doubt that our Saltdean station (XXV.), which is but a few feet above the sea, must receive more spray than the sheltered Saddlescombe colonies, but it shows very few melanics. We are equally at a loss to explain the absence of dark forms from exposed stations on the coast of Somerset and W. Ireland. It is possible that these exceptions might be explained away by appealing to some deviation in the direction of the wind, but we hardly believe that this is likely to be successful. On the whole, then, we are as sceptical as to this hypothesis as to the first.

There remains the question of "insular melanism." The high prevalence of melanism on many islands is in favour of its being due to some factor (spray or moisture) specially characteristic of islands. It is very interesting indeed to note that the only place in the Mediterranean region from which we have obtained melanics is from the Balearic Isles. Actually nearly all the islands situated elsewhere from which we have received specimens show a high percentage of melanism. The only exceptions are the Isle of Wight (Freshwater) and Corsica. In each case the total number of specimens is rather low (Freshwater, 29; Corsica, 22). Two small series from N. Uist and Colonsay (14 specimens in all) contained 21·4 per cent. melanics, which is rather low as compared with the frequency on other islands. On the whole,

however, our data tend to confirm the "insular" hypothesis. We are, however, unwilling to accept the current explanation (salt spray and moisture) in view of what has been said above, for in essence an insular habitat does not differ in exposure from a littoral mainland one, and we have reason to doubt the effect of these factors in the latter.

As regards differences of temperature, we certainly think that this can be disregarded as a cause of the melanism reported here. The differences in temperature between, *e. g.*, Weymouth (melanism frequent) and Sussex (melanism rare) or between the Scilly Isles and Braunton (N. Devon), which show the same contrast in the frequency of melanism, are insufficient to account for the differences in pigmentation.

If our extreme scepticism is met with by the suggestion that our alleged anomalies may be explained by the possibility that our non-melanic populations (*e. g.*, at Freshwater) are new-comers, and have, therefore, had no time to be affected, we have only to point to the long period during which the Freshwater colony has been known.

Although we have expressed ourselves sceptically as to the effects of spray-borne salts, we would suggest that the clue to the local differences in the incidence of melanism might be the presence of some food-plant or plants which selected the melanism-inducing salt from the soil, and that the presence of such salts might be determined by geological formations as well as by the amount of spray.

It remains to say a word about the results and views of Kammerer (1926—see Summary, p. 250 and following), who experimented with and described the dark forms of *Lacerta* from the Dalmatian Archipelago. He says of these forms (*l. c.* p. 257): "Dunkle Färbungen sind durch kombinieste Intensität de Lichtstrahlung, Hitze und Dürre enstanden." It is interesting to notice the following points:—

1. In Lizards of the Mediterranean area the melanic condition is evoked by the excessive sunlight, heat, etc., in more or less unprotected island-habitats.

2. Kammerer (*l. c.* p. 178) found that dark forms of *Eobania* [*Helix*] *vermiculata* and *Helicella variabilis* can be produced by high temperature ("bei ansteigender Temperatur").

3. Nevertheless we find that the Mediterranean region, an area of stronger sunlight, greater heat, and dryness than N.W. England, is more deficient in melanic *Cochlicella acuta* than N.W. England. In the Mediterranean region melanic *Cochlicella acuta* only attains a high frequency on *some* islands (Balearics).

4. The difference between the amount of melanism in the insular and mainland *Cochlicella acuta* in the Mediterranean and, on the other hand, the paradoxical fact that, though high temperature (*fide* Kammerer) produces darkening in *Eobania vermiculata* and *Helicella variabilis*, *Cochlicella acuta* is lighter on the Mediterranean seaboard and darker in N.W. England, are not easily explained. Kammerer (*l. c.* p. 252), however, points out that the various characters and groups of organisms which he studied do not always exhibit the same varietal tendency ("Ein Beispiel für ersteres liefert *Lacerta serpa pelagosæ*, deren Grundfarbe sich aufhellt, deren Zeichnung sich verdunkelt, ... ferner neigen *L. serpa*, *fiumana* und *oxycephala* auf den Scoglien um Lissa zur Verdunkelung, *Euscorpius carpathicus* dagegen zur Aufhellung").

Summary.

1. *General.*

(1) The colour-pattern of the shell of *Cochlicella acuta*, a Palæarctic Helicid land-snail, is described. The chief modes of variation are indicated and the shell-

structure and the causes of pigmentation are discussed. An account is given of the distribution and origin of melanic forms.

(2) The local variation of the pattern in nine colonies of the species situated in south and south west Sussex is described in detail. A larger geographical series, including specimens from the west and eastern littoral of the Mediterranean, is more summarily dealt with.

(3) The amount of statistically significant difference between the colonies in Sussex is determined, and its causes and general importance are discussed.

2. *Habits and History of the Species in Sussex.*

(4) *C. acuta* is a Lusitanian species usually inhabiting dunes and grassy places close to the sea. Sporadic local invasions of inland habitats has taken place.

(5) It seems to have invaded Sussex at a relatively recent date, and, though it may have had a wider range in this county in the middle of last century, it is now highly localized.

(6) All the known colonies were probably formed within the last fifteen years, except that at Burpham. The species is probably liable to accidental transport (probably by human agency), though changes in agricultural practice and the attacks of a parasitic dipteran may influence its local appearance and disappearance.

3. *Intercolonial Variation.*

(7) The habitats of the Sussex colonies are described, and the local variation of the characters investigated is held to be independent of environmental factors.

(8) Differences due to age are found to be negligible in so far as the intercolonial differences in pattern are concerned.

(9) The various colonies differ "significantly" one from another in about 36 per cent. of the possible comparisons.

(10) Significant annual change occurs in half the colonies studied over 8–2 years. The amount of change is not large, and 72 per cent. of the possible character-comparisons show no change in the period of observation.

(11) It is held that the differences between the colonies are due to the latter having been derived from different sections of the original population and to the sorting-out of the different hereditary tendencies of the latter in isolated and localized communities.

4. *Melanism.*

(12) Melanism is characteristic of *Cochlicella acuta* in the western parts of the British Isles, and practically absent in the continental littoral of the Mediterranean. It is found well developed on small islands.

(13) Though the general distribution of melanic forms seems to suggest a correlation of melanism and atmospheric humidity, the local distribution of dark forms is capricious, and other factors (?halophilous plants, spray-borne salts, geological formation) may be collectively responsible for, or contributory to, their origin.

Bibliography.

Alkins, W. 1928. The Conchometric Relationships of *Clausilia rugosa* and *Cl. cravenensis*. Proc. Malac. Soc. xviii. pt. ii. p. 50.

Aubertin, D. 1927. On the Anatomy of the Land Snails *Cepea hortensis* and *Cepea nemoralis*. Proc. Zool. Soc. p. 553.

Bofill, A., & Haas, F. 1920. Estudi sobre la malacologia de les valles Piranaiques.—V. Treb. Mus. Cienc. Nat. Barcelona,

BÖTTCHER, G, 1913. Die männliche Begattungsweillzeuge Bei... *Sarcophaga*. Deutsche Ent. Zeitschr. p. 351.

BOULENGER, G. A. 1913. Second Contribution to our Knowledge of the Variation of the Wall-Lizard. Tr. Zool. Soc. London, xx. p. 135.

BOURGUIGNAT, M. 1860. Malacologie ... de la Bretagne. Paris.

BOYCOTT, A. E. 1919. Observation on the Local Variation of *Clausilia bidentata*. Journ. Conch Leeds, xvi. no. i. p. 10.

——— 1927. Further Observations on the Local Variation of *Clausilia bidentata*. Journ. Conch. Leeds, xviii. no. v. p. 131.

CRAMPTON, H. E. 1916. Studies on the Variation, etc., of the genus *Partula*. Pub. Carn. Inst. Washington, No. 228.

——— 1925. *Ibid.* Pubn. No. 228 *a*.

DEAN, J. D. 1923. Observations on the Land Mollusca of the Coasts bordering on the Bristol Channel. Journ. Conchology, xvii. p. 57.

DISTASO, A. 1908. Die Beziehung zwischen der Pigmentbändern des Mantels und denen der Schale bei *Helix*... Biol. Centralbl. xxviii. p. 120.

DUPUY, D. 1849. Histoire naturelle des Mollusques terrestres, &c., qui vivent en France. Paris.

ELLIS, A. E. 1926. British Snails. Oxford.

FAGOT, P. 1883. Glanages malacologiques, p. 29. Toulouse.

GAMBETTA, L. 1929. Ricerche faunistiche nelle isole italiane dell' Egeo. Arch. Zool. Ital. xiii. p. 45.

GERMAIN, L. 1903. Étude sur les Mollusques ... des environs d'Angers, etc. Bull. Soc. Sci Ouest France, (2) iii. p. 131.

——— 1906. Études sur quelques mollusques ... du massif Armoricain. Bull. Soc. Sci. Nat. Ouest France, (2) vi. p. 54.

——— 1908. Étude sur les Mollusques récueillis en Khroumirie (Tunisie). Voy. Zool. en Khroumirie [d'H. Gadeau de Kerville].

——— 1921. Voyage Zoologique d'Henri Gadeau de Kerville en Syrie, tom. ii.

——— 1928. Sur le mélanisme chez les Mollusques. Journ. Conchyliologie, lxxii. p. 127.

GEYER, D. 1927. Unsere Land- und Süsswasser Mollusken. Stuttgart.

GÖRNITZ, K. 1923. Ueber die Wirkung klimatischer Faktoren auf die Pigmentfarben der Vogelfodern. Journ. f. Ornithologie, Bd. lxxi. p. 456.

HARRISON, J. H., & GARRETT, F. The Induction of Melanism in the Lepidoptera. Proc. Roy. Soc. London, B, xcix, p. 241.

HARRISON, J. W. H. 1920. Genetical Studies in ... *Oporabia*... Journ. Genetics, ix. p. 195.

HARTMANN —. In Sturm's Deutschlands Fauna.– VI. Die Wurmer.

HIDALGO, J. 1875. Catalogo ... de los Moluscos Terrestres de España.... II.

KAMMERER, P.1926. Der Artenwandel auf Inseln.... Vienna.

KEILIN, D. 1919. On the Life-History of ... Diptera living on Molluscs. Parasitology, xi. no. 3, p. 430.

KENNARD, A. S. 1923. The Holocene Non-Marine Mollusca of England. Proc. Malac. Soc. xv. p. 241.

——— & WOODWARD, B. B. 1901. The Post-Pliocene Non-Marine Mollusca of the South of England. Proc. Geol. Assoc. xvii. pt. 5, p. 213.

JEFFREYS, J. G. 1862. British Conchology, i. London.

JENNER, J. H. 1884. List of the Land and Freshwater Mollusca of E. Sussex. Trans. Eastbourne N. Hist. Soc. pt. viii. i. p. 44.

LOCARD, A. 1882. Catalogue général des Mollusques vivants de France. Paris.

MANDOUL, H. 1903. Recherches sur les colorations tégumentaires. Ann. Sci. Nat. (8), xviii. p. 225.

MANSELL-PLEYDELL, J. C. 1898. The Mollusca of Dorsetshire. Dorchester.

MERMOD, G. 1930. Catalogue des Invertébrés de la Suisse.

MERTENS. R. 1924. Ein Beitrag zur Kentniss der melanotischen Inseleidechsen des Mittelmeeres. Pallasia, ii. 1. p. 40.

MOQUIN-TANDON, A. 1855. Histoire Naturelle des Mollusques Terrestres &c. de France, ii. Paris.

MOBEY, F. 1909 (Ed.). A Guide to the Natural History of the Isle of Wight. London.

MOUSSON, F. 1854. Mitt. Naturf. Ges. Zurich, no. 103, p. 393.

——— 1859. Coquilles Terrestres et Fluviatiles récueillies dans l'Orient... Zurich.

——— 1863. *Op. cit.* pt. ii.

NOBRE, A. 1909. Faune malacologique des possessions portugaises de l'Afrique occidentale. Bull. Soc. Port. Sci. Nat. iii. Supp. 2, p. 1.

PALLARY, P. 1909. Catalogue de la faune malacologique de l'Egypte. Mem. Inst. Egypt. vi. fasc. 1.

PILSBRY, H. 1888. A Manual of Conchology, (2) iv. p. 31.

——— 1894. *Ibid.* (2) ix. p. 263.

RENSCH, B. 1928. Inselmelanismus bei Mollusken. Zool. Anz. lxxviii. p. 1.

——— 1929. Das Prinzip Geographische Rassenkreise, etc. Berlin.

RICE, R. G. 1930. In Ed. Notes. Journ. Conchology, p. 26.

ROBINSON, M. 1918. Wild Life on the South Downs. Abstracts, Brighton & Hove N. Hist. & Phil. Soc. p. 37.

RZYMOWSKA, T. 1914. Contribution à l'étude... de *Helix barbara*. Rev. Suisse Zool. xxiii. p. 277.

STATUTI, S. 1882. Catalogo... dei Molluschi... viventi nella provincia Romana. Siena.

STELFOX, A. W. 1911. A List of the Land and Freshwater Molluscs of Ireland. Proc. Roy. Irish Acad. B, no. 3, p. 65.

——— 1912. Clare Island Survey, pt. xxiii. Proc. Roy. Irish Acad. xxxi., p. 1.

STEP, E. 1927. Shell Life. London.

STUBANY, R. 1902. Verh. zool.-bot. Ges. Wien, lii. p. 381.

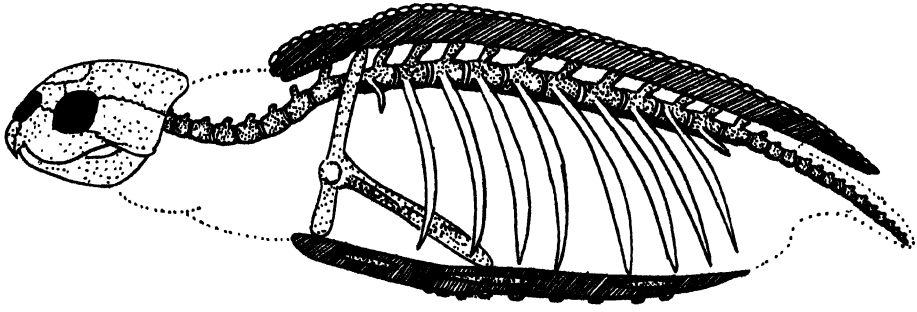
TOMS, H. S. 1922. *Cochlicella acuta* in Sussex. Brighton & Hove Nat. Hist. & Phil. Soc. Repts. p. 1.

WESTERLUND, C. 1871 Fauna Molluscorum, etc., Sueciæ, etc. Stockholm.

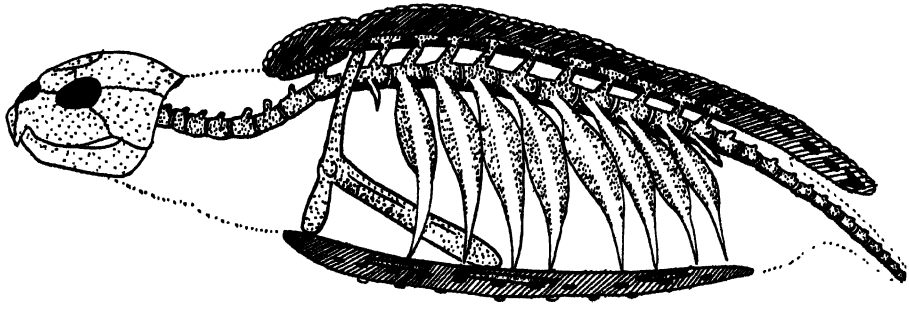
PLATE I.

Examples of shell-pattern in *Cochlicella acuta*.

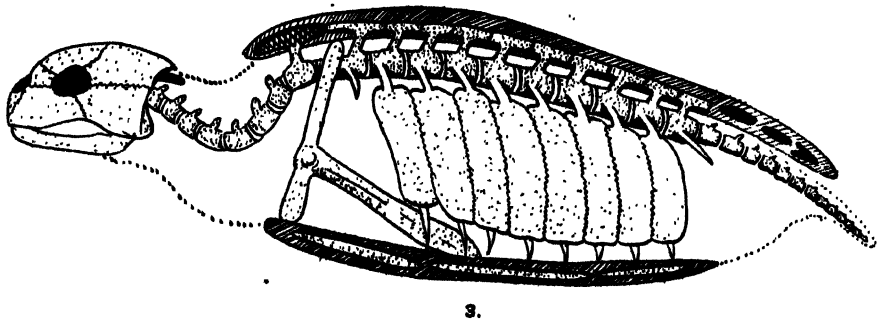
Figs. 1–5. Unbanded forms, Class A.
6–8. Banded and flammulate forms, Class B^2.
9–12. White and banded forms, Class B^1.
13–15. Melanic shells.
Fig. 16. Longitudinal section of a banded shell.



1.



2.



3.

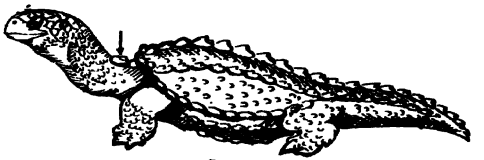
P. E. P. Deraniyagala, del.

John Bale, Sons & Danielsson, Ltd. London.

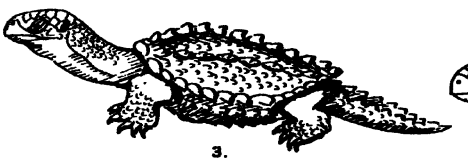
TESTUDINATE EVOLUTION.



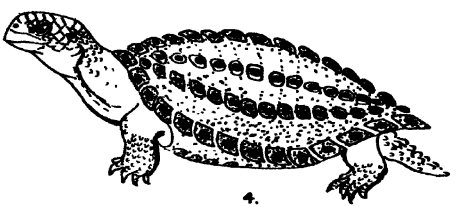
1.



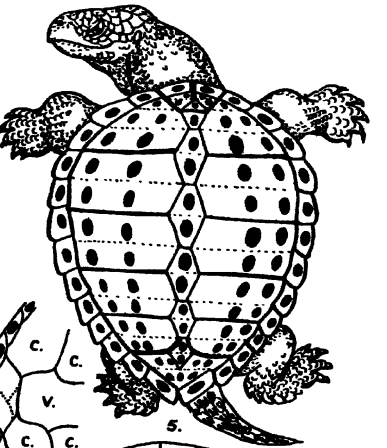
2.



3.

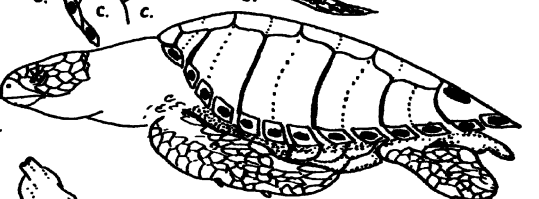


4.

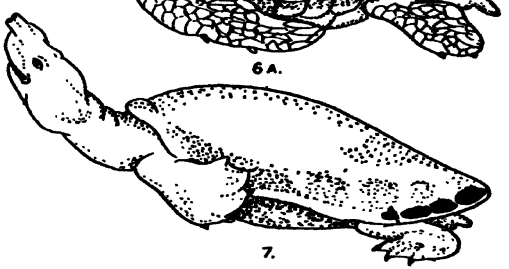


5.

6.



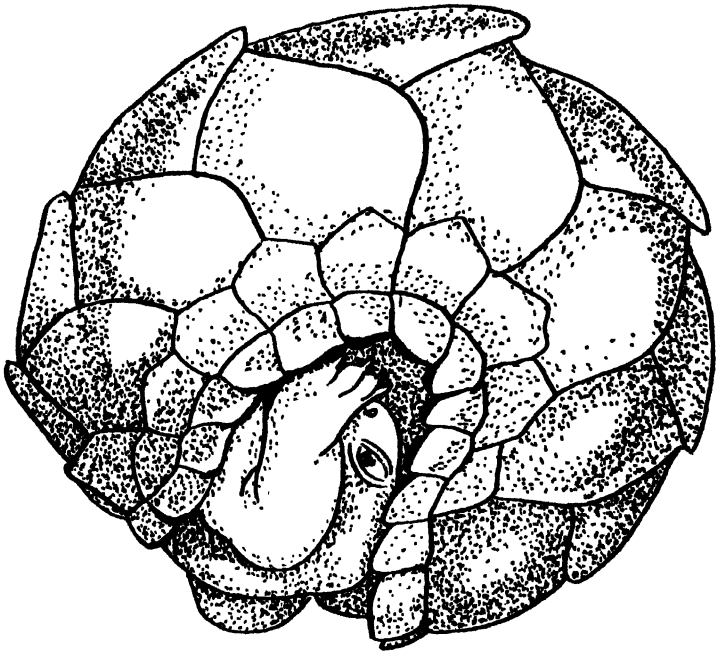
6A.

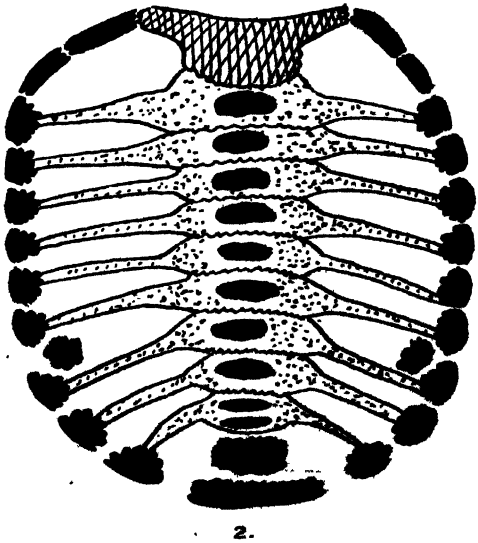


7.

P. E. P. Deraniyagala, del

John Bale, Sons & Danielsson, Ltd. London.





2.

P. E. P. Deraniyagala, del.

John Bale Sons & Danielsson, Ltd. London

TESTUDINATE EVOLUTION.

50. Testudinate Evolution. By P. E. P. Deraniyagala, M.A.Cantab., A.M.Harvard *.

[Received May 1, 1930: Read June 3, 1930.]

(Plates I.–III.†)

It was while preparing a systematic paper on the Testudinata of Ceylon that the writer's attention was drawn to the remarkable changes within the species in an order where several minor characters remain curiously constant. The present paper is an attempt to explain these characters and also those structures peculiar to this order from data collected after an examination of fossils, embryos, and adults.

The writer wishes to offer his sincere thanks to Prof. J. Stanley Gardiner for his generosity in permitting the free use of the Cambridge laboratory, Mr. C. Foster Cooper for X-ray photographs of *Dermochelys*, Dr. J. Parrington for advice in section staining, Dr. Malcolm Smith and Mr. H. W. Parker, of the British Museum, for permitting him to examine their valuable collection, and Prof. D. M. S. Watson, of London University, for his kindness in reading over this paper and examining the specimens mentioned therein.

The material used for this paper consisted of *Dermochelys coriacea* (Linné), *Emyda granosa ceylonensis* (Kelaart), *Geoemyda trijuga thermalis* (Lesson), and the Cheloniidæ. Specimens from other countries and fossils in the Cambridge and British Museums were also examined.

The methods of investigation were:—(1) Sectioning and staining with iron alum and hæmatoxylin, and counterstaining with carbol fuchsin or a modification of Zeihl's fuchsin method suggested by Dr. Parrington. (2) The use of alizarin and potash solution to stain the osseous portions of embryos *in situ*. Then clearing the specimens in glycerin, cedar oil, or xylol, when the deep red osseous parts were easily seen. This method proved to be most useful, as there was no room for error through distortion of the tissues, bad fixation, or bad sectioning.

Testudinate evolution has engaged the attention of scientists for over a century, but whilst many new problems have arisen, the original ones still remain unsolved. For a better understanding of the subject a brief summary of the chief features of this order is necessary, and the parts of a Testudinate may be described as follows. The carapace and plastron form the "corselet," the fore limbs may be termed "arms," the hind limbs "legs." The horny covering of the corselet consists of "scutes," under which lie bony plates. The horny covers of the jaws are "beaks." The vertebral column and ribs are the "endoskeleton."

The order Testudinata has ten ribs, of which the first and last pairs are rudimentary, supporting a carapace which, together with the ventral plastron, forms a corselet consisting of numerous osseous plates sutured together under which the head, limbs, and tail are more or less retractile. The scapular and pelvic girdles are inferior to the ribs, not superior, as in other vertebrates. A nuchal bone is always present. Four horny dorsal scutes usually present along each side, absent in some. Jaws in beaks, edentulous. Reproduction oviparous. Two suborders, the Atheca and Thecophora.

* Communicated by Prof. D. M. S. Watson, F.R.S., F.Z.S.

† For explanation of the Plates, see p. 1070.

The Atheca have a corselet of ossified dermal scales which are separate from the endoskeleton. Nuchal bone, ribs, and vertebræ free. Plastron with eight bones, the entoplastral element being absent. No endoskeletal expansions. A single species highly modified for marine life.

The Thecophora have a corselet formed by the nuchal bone, endoskeleton, and nine plastral bones which are bound up in dense dermal tissue. In the mature embryo, or after birth, these bones form expansions which invade the dermal tissue matrix, which they finally replace more or less completely*. Nuchal always fused to the last cervical vertebra in the adult. Numerous families, terrestrial, amphibious, aquatic, or marine.

Many theories have been advanced to explain the development of the various peculiar Testudinate structures. The prevalent ones are:—

(1) The Thecophoran carapace is formed from expansions arising from the ribs and vertebræ fusing with the dermal bones, such as the nuchal, marginals, and pygals. In the Atheca these endoskeletal expansions disappeared, and the marginals proliferated to form a protective mosaic of platelets.
(2) The plastron consists of the entoplastron derived from the interclavicle, the epiplastra from the two clavicles, the remaining bones arising from the gastralia (abdominal ribs) of the primitive ancestor.
(3) The origin of the scutes is unknown.
(4) The shoulder-girdle lies beneath the ribs and (*a*) the stumpy embryonic ribs follow pre-existing grooves in the dermal carapace, and are thus prevented from descending to their normal position below the girdle; (*b*) the shoulder-girdle developed a columnar form and slipped between rib and rib into the body-cavity.

Investigation of the problem of Testudinate evolution is commenced with a study of palæontology which too often has developed into a snare, owing to the incomplete sequence of fossils. A salient feature is that the vast majority of Testudinate fossils are Thecophoran. Curious as this may seem, their abundance is easily explained by watching the disintegration of the recent corselets of the two suborders. The comparatively cartilaginous Athecan, which is loosely sutured together in small units, speedily falls apart and is scattered; but the Thecophoran, which is osseous and composed of firmly sutured large units, remains together for a considerable period, thus having a greater chance of fossilization. Therefore it was only under exceptional circumstances of rapid burial that Athecan fossils were formed.

The earliest known fossil which has been claimed for the Testudinate is *Psephoderma alpina* von Meyer, from the Bavarian Triassic. It is Athecan in structure and is a portion of the corselet. This has been claimed as a fossil crocodile by some, as a Placodont by others. *Proganochelys quenstedtii* Baur is also Triassic and is completely Thecophoran. Superimposed on the carapace are smaller platelets forming a supramarginal series. Another Thecophoran, *Archelon ischyros* Wieland (Pl. III. fig. 2) shows a row of epineural platelets lying above the neural plates, and also a rudimentary supramarginal row. *Toxochelys bauri* Wieland, a Thecophoran, has the epineurals reduced to three or four, while the supramarginals have disappeared completely.

If *Psephoderma* be disregarded, Athecan fossils appear only in the more recent strata, and the ventral armature, which is complete in the earlier forms, begins to disappear in *Psephophorus polygonus* von Meyer, from the Pliocene, while in modern Dermochelys it is rudimentary and at times altogether absent. This would indicate that the Atheca have existed for a long period in water and have

* Wherever the skeletal bones touch the dermal corselet, secondary osseous callosities arise possibly through friction between the skeletal bones and thick dermis.

begun to dispense with their osseous armature, recent forms having less than fossil forms. The fossil Thecophora show that there were numerous longitudinal rows of platelets lying upon the Thecophoran corselet, or, in other words, the corselet formed of endoskeletal expansions had rows of dermal bones lying on it (Pl. III. fig. 2) which later began to disappear.

The origin of these dermal bones is of great value in recasting the evolution of the order. The writer, working with embryo *Caretta*, found that the marginals formed deep down in the dermal carapace, and Versluys mentions that Menger found that the marginals of *Emyda* arose similarly *.

Sections through the carapace of an adult *Dermochelys* disclosed that the Athecan platelets arose in the upper layers of the dermal corselet, very near the surface, and not in the lower layers, as is the case with Thecophoran marginals. Hence modern Testudinata show three layers of ossification (Pl. I.):—

(1) An upper dermal layer of platelets in the Atheca (fig. 1).
(2) A lower dermal layer of platelets in the Thecophora (fig. 2).
(3) A layer of endoskeletal expansion in the Thecophora (fig. 3).

Fossil evidence tends to show that when bone comes in contact with bone the upper layer is replaced by the lower. Hence it is reasonable to suppose that the external Athecan platelets were replaced by the deeper Thecophoran platelets, which were, in turn, replaced by the endoskeletal callous expansions wherever they came in contact.

Confusion between the upper Athecan and deeper Thecophoran platelets has been responsible for the theory that the Athecan corselet is derived from a proliferation of Thecophoran marginals. Coupled with this is an imperfect knowledge of the function of the nuchal bone, which is the first dermal bone to appear. A series of embryos of *Dermochelys* and Thecophora stained in alizarin showed the order of ossification to be as follows:—(1) Endoskeleton and plastral bones; (2) nuchal; (3) marginals appeared anteriorly and extended posteriorly; (4) endoskeleton and plastral bones began to form callous expansions; (5) pygals; (6) the nuchal was pushed up by the last cervical vertebra and fused with it in the Thecophora.

The nuchal bone is phylogenetically one of the most important structures in the Testudinata, which is the only order to possess this feature. It is the direct result of the retractile neck, and is an anchor to such retractile muscles as the testo-occipitis, longus-colli, and testo-cervicalis, which Burne on dissecting *Dermochelys* found to have their origin in this bone. In all probability the nuchal bone is derived from a co-ossified cluster of epidermal nuchal scales as are present in modern Crocodylia, denoted in Pl. II. fig. 1 by an arrow. The retractile neck action conflicted with the humping up of the shoulders anteriorly to form a nuchal fold, the anterior margin of the future carapace, and it was under this fold that the nuchal base was carried and left behind by the retractile neck (Pl. II. fig. 2, arrow). This transfer of the nuchal scales was partly to avoid chafing and friction resultant on the telescoping neck, partly to increase the value of the nuchal as a muscle anchor by fixing it in the carapace tissue.

Its attachment to the ventral side of the dermal carapace is well marked in *Dermochelys* both young and old, and the bone can easily be torn out of an adult carapace, with the hand, after putrefaction has loosened the layer of connective tissue which holds it in place. Its ventral attachment is also conspicuous in young *Emyda granosa ceylonensis*, but in the adult it is pushed up. With the transformation from the Athecan to the Thecophoran the curvature of the spine

* It was not till the specimen had been clearing for some time in glycerin that the marginals appeared to view, and dissection showed them to be deep-seated.

increased, and thereby brought the neural process of the last cervical vertebra into intimate contact with this bone, which was pushed up until it touched the two anterior marginal bones, which it soon displaced. In some forms such as *Caretta caretta* (Linné) the nuchal bone, instead of being covered by a single nuchal scute, often shows the primitive covering of two contiguous marginals and a small vertebral scute posterior to these, clear proof that these three platelets were supplanted by the nuchal, which was pushed up beneath them (Pl. II. fig. 6). Besides, there are several fossils which show dermal Thecophoran platelets lying upon the neural plates; many in some forms, reduced in others, until they disappeared completely, replaced by the neural expansions, which were pushed up against them from below (Pl. III. fig. 2). The nuchal bone increased its firmness in the Thecophora by fusing with the neural spine of the last cervical vertebra and with the contiguous endoskeletal callous expansions. This was necessitated by the greater stresses imposed on this bone, as the Thecophora, which were all terrestrial during a part of their evolution, depended for safety on the rapid withdrawal of the head into the corselet, whereas in a marine type, as the Atheca, speed of locomotion dispensed with the necessity for retraction into the corselet, while after a time the neck became short, thick, and stiff, to give the animal a torpedo-shaped contour, to enable rapid progress through water influenced by waves and currents.

As seen from the condition of the nuchal bone, the Atheca took to water before the retractile powers of the neck had developed as highly as in the Thecophora, and once marine, development in this direction ended, and the nuchal bone continued to remain in the stage it was when the animal first took to water.

Embryological evidence, as seen by Parker in *Chelonia mydas* (Linné) and by the writer in *Dermochelys coriacea* (Linné) and in *Caretta caretta* (Linné), shows a lizard-like form with a well-developed lateral fold on each side, beneath which lie the limbs which project and are in no way deep set. Later the nuchal fold appears, marking the anterior boundary of the carapace, and the embryo commences to widen laterally. The pygal area is confluent with the caudal area, and is the last part of the carapace to differentiate itself. The early appearance of the nuchal bone prior to any of the dermal corselet bones shows that the retractile neck developed early in the history of the Testudinata. As all reptiles are covered with scales, it is reasonable to suppose that the ancestral form was similarly provided with subequal scales, which later differentiated into large and small, as seen on the flippers and heads of modern Cheloniidæ. When the retractile habit developed, the body scales ossified to form a protective corselet, the boundaries of which were the nuchal fold produced by the interaction of the neck retracting posteriorly against the shoulders, which humped up anteriorly; while the lateral dermal fold, common to lizards, was the seat of the future marginals, and gradually the carapace extended posteriorly to shelter the hind limbs and tail (Pl. II. fig. 3). The order of formation of the corselet is :—

(1) Nuchal bone shifted under dermal corselet, which was covered with Athecan platelets (Pl. I. fig. 1).

(2) Athecan platelets replaced by deeper Thecophoran platelets, which arose in the longitudinal corselet ridges (Pl. I. fig. 2).

(3) Endoskeleton forms expansions, and wherever these come into contact with the Thecophoran platelets replaces them (Pl. I. fig. 3).

(4) Nuchal is pushed up by the neural process of the last cervical vertebra in the Thecophora, and fuses with the endoskeletal expansions behind it. As the endoskeleton does not come into contact with the marginals or Thecophoran platelets of the pygal area, these latter persist in modern Thecophora.

Palæontology has revealed certain characters to be primitive, and are generally accepted as such to-day by the majority of scientists:—

(1) The roofing of the temporal region of the skull is primitive; later the roof is lost through emargination from behind.—*Watson.*
(2) The primitive skull is palæorbital, and in it the frontal bone does not enter the orbital rim (Pl. I. fig. 1). The recent or neo-orbital has the frontal forming part of the orbit (Pl. I. fig. 3).—*Nopcsa.*
(3) A large parasphenoid separating the pterygoids is primitive.—*Versluys.*
(4) The presence of inframarginal scutes is primitive.
(5) Ossicles or large scales on the tail is primitive.
(6) Accessory bony platelets on the corselet, as in extinct forms, is primitive. Some modern forms are said to show faint traces of such, but this is open to doubt.

Now, with this knowledge it is possible to attempt reconstructing the ancestral form:—

(1) The skull had the temporal region roofed over. It was palæorbital and had a secondary palate partially developed, as seen in fossils.
(2) The nuchal bone was free.
(3) The skeleton had no expansions.
(4) The plastral bones had already arisen from the clavicles, interclavicle, thoracic ribs, and gastralia, but the hyo- and hypo-plastral bones did not overlap as yet. This is the condition in the mature embryo which is doubled up over the yolk in a line of flexure extending between these bones and dividing the plastron into thoracic and abdominal areas.
(5) The corselet was dermal and covered with ossified scales, as seen in young *Dermochelys.*

The original Protestudinate was probably palustrine, and carried three dorsal shields of osseous scales: the nuchal on the neck, the tergal or dorsal on the back, and the caudal (Pl. III. fig. 1). These appear to have been strengthened by single rows of enlarged scales, and, judging from fossils and newly-hatched *Dermochelys*, there was a well-developed ventral armature of osseous scales, similar to that found in the modern Caiman. As the animal commenced to retract its neck and limbs, the osseous scales upon them ceased to be useful, and caused irritation by chafing as these members telescoped into safety within the corselet. Hence they gradually disappeared unless, as in the case of the nuchal, they were needed (Pl. II. figs. 2, 3). The body corselet persisted, and the only marks of the previous existence of ossified scales on neck or limbs were probably denoted by longitudinal colour bands, which were continuous with the bands on the corselets and to-day occupy the rows of enlarged scales in young *Dermochelys*. The tail alone did not telescope, but was bent in sideways under the carapace, and has continued to be protected thus to this day. This was effected by one bend at the base of the tail in contrast to the numerous bends prior to retraction. As can be perceived, the tail was subjected to much less friction than the other members. Hence prominences such as ossicles or scales persisted on the tail, although absent from the head and neck, and also remain to some extent on the distal parts of the limbs which are not subject to friction, *e.g.*, the Chelydridæ have ossicles on the tail, and *Carettochelys*, a smooth-skinned form, has large dorsal scales on the tail and four vestiges on the front margin of each fore limb.

At this early stage the protestudinate corselet was entirely dermal with an external protective layer of ossified scales. The powers of retraction were limited and chiefly confined to the neck, while the animal shrugged its shoulders over its

head for protection, as do modern Cheloniidæ, which suffer from a secondary loss of this power of retractility. Gradually the dermal corselet defined its boundaries as the powers of retractility of the limbs developed the lateral fold, often so well marked in modern lizards, formed the two sides of the carapace, which, as seen from the developing embryo, ultimately projected posteriorly, forming a shelter for the tail.

During this process the dermal corselet began to assume intimate contact with the endoskeleton, while the posterior portion of the carapace was supported by some of the posterior ribs which elongated until they sheltered the pelvic girdle. As frequently occurs when skin comes into close contact with bone, it began to thicken and stiffen, and in so doing pressed down on the endoskeleton. The shoulder-girdle, which hitherto lay in the normal reptilian position, found itself becoming constricted between these two. To remain in its original position would presently render it immobile and force it to ankylose with the ribs; the only alternative was to shift to a position where the skin was more flexible, and where there would be a greater depth of soft tissue between the dermis and skeleton. Such conditions existed towards the base of the neck; so, aided by the shrugging shoulders as they protected the head, the pectoral girdle migrated anteriorly past the first rib. As the forequarters developed a permanent protective hunch, the scapula slid over the front ribs and attained a vertical position, bringing its distal end in contact with the carapace in the interspace between the nuchal bone and rudimentary first rib (Pl. I.). Thus it will be noticed that, although the scapula shifted, its position still remains *external* to the ribs, as it is in front of the first rib. It was impossible for the scapula to revert to its original position, as the dermal carapace was in intimate contact with the ribs; so in order to strengthen its comparatively superficial position, it developed osseous prolongations which advanced back into the body-cavity. These are the new acromium process and the enlarged coracoid which had no obstacles to bar their backward progress, as the interclavicle and clavicles were separate from the skeleton and embedded in the plastron. These new bones were of use both to strengthen the position of the scapula and also combined with it to form a tripod to keep the carapace apart from the plastron, and for this purpose the scapula changed from a flat bone to a cylindrical one. The attachment of the scapula to what is really the nuchal fold of the carapace was observed in X-ray photographs of *Dermochelys* as well as in cleared specimens of all the Ceylon forms. Supporting the view that the acromium and coracoid are secondary prolongations posteriorly is the statement by H. Ruckes, who, whilst maintaining that the pectoral girdle has not shifted, finds on sectioning embryos "There always persists a much reduced remnant of the body-wall between the girdle elements and the body-cavity proper." This plainly shows that the secondary developments of these bones must have bent the body-wall into the cœlomic space.

The animal now had a dermal corselet covered with ossified dermal scales, while the pectoral and pelvic girdles lay partially sheltered by the ribs. At this stage one branch took to water, never to abandon it. This gave rise to the Athecæ. The remainder gradually became terrestrial at varying intervals and formed the Thecophora. The sun's rays and altered conditions of terrestrial existence produced a gradual stiffening of the dermal corselet, and with the change of habitat the Thecophora relied more than ever on hunching themselves up, and evolved an armadillo-like habit of rolling up into a ball after retracting the neck and hunching the shoulders over the head. They were enabled to do this because at this stage the hyo- and hypo-plastral bones of the adult did not overlap, but remained apart as they do in the embryos of modern Thecophora. The dermal corselet was divided into strips by transverse lines of flexure or sulci, which developed between the ribs and facilitated the process of coiling up for protection. (Pl. III. fig. 1.)

The ossified dermal scales, hitherto common to the Atheca and Thecophora, soon proved insufficient protection for the slow-moving terrestrial form, and larger secondary bony platelets developed deep in the thick longitudinal dermal ridges of the corselet. They appear to have been confined to the ridges, as probably the carapace skin was not deep enough elsewhere to permit of their development. The upper Athecan ossified scales were entirely replaced by the Thecophoran platelets of deeper dermal origin, and the former soon ceased to exist. Probably the Thecophoran secondary platelets underwent considerable reduction until the minimum of fourteen marginals was reached. This is the largest known number of marginals present on one side of a Thecophoran, viz., *Caretta*, whereas young *Dermochelys* shows twenty-eight to thirty enlarged dermal marginal scales.

But even these platelets were insufficient protection, and so those skeletal bones which came into contact with the dermal corselet formed callous-like expansions. As these expanded, the dermis became stiffer and more corneous in proportion to the surface of bone brought in close contact with it, and the scutes became completely keratinuous as in modern Thecophora.

Embryos of modern Thecophora show the soft vascular dermis divided into scutes long before the appearance of dermal bones or any skeletal expansions, and it is only with the formation of these expansions that the Thecophoran scutes become entirely keratinous. Fossil evidence amply proves the presence of the Thecophoran platelets which lie on the skeleton in such forms as *Proganochelys*, *Toxochelys*, the Protostegidæ, and *Archelon*, and it is significant that where the skeletal expansions are slight, these platelets are most abundant and are fewest on those forms which possess advanced skeletal expansions.

In the stage where the Thecophoran protected itself by rolling up, sulci split the dermal corselet covering into scutes. Now, the marginal edge required a maximum of flexibility to enable constriction to as close a compass as possible when the animal coiled itself up. Hence there was a sulcus between every two marginal platelets. As such flexibility was not necessary for the rest of the carapace, the other divisions were larger. The inframarginals, and when present the supramarginals, are fewer and larger than the marginals, while the costal and vertebral scutes are largest of all. This was caused by fusion of some of the scutes, and gradually the minimum number of three sulci and four costals was reached. This explains the nearly constant presence of four costal scutes in the vast majority of Thecophora while there are more costal plates than scutes, whereas the marginal plates equal in number the marginal scutes. The Thecophoran ridge platelets underwent a similar reduction into larger and fewer platelets before they finally disappeared. The plastron, which had to be encompassed by the carapace and hence forced to assume smaller dimensions, also retained more dividing sulci than the carapace. At a later date the first pair of marginals were replaced by the nuchal bone, which was pushed up against them, and with their loss the marginal scutes shifted up accordingly and disarranged their original position with regard to the marginal plates, and this was further enhanced by the increasing curvature of the carapace. Gradually friction against the ground and other causes stiffened the plastron, while now the endoskeletal expansions were so advanced that they became juxtaposed osseous plates which eventually were to replace entirely the Thecophoran platelets. It was then that the coiling-up habit was dispensed with, and the animal depended solely on retraction into its hard corselets, while at this stage the ends of the hyo- and hypoplastra overlapped in the adult, as they do in all modern Testudinata. The sulci of the "armadillo" stage persisted in spite of the loss of the coiling-up habit. There were two chief stimuli which assisted in the retention of the sulci—the curvature of the embryo round the yolk and the existence under terrestrial conditions which originally stiffened the dermal corselet. The stimulus derived during the

embryonic period loses its potency in old age, when the scutes tend to fuse until in very old specimens they are almost indistinguishable. The terrestrial conditions fail to act on forms which have remained aquatic for long periods, and the scutes, which are no longer needed by the now fast-moving animal, disappear as they have done in the Trionychoidea and *Carettochelys*.

The arching of the carapace, the numerical reduction of the costal and vertebral scutes by fusion, the pushing forward of the marginal scutes after the anterior pair had been supplanted by the nuchal, have all tended to disarrange the original position of the scutes, and it is the marginals alone which provide a clue to solving the incongruities displayed between the costal scutes and their underlying plates. Pl. II. fig. 5 shows the carapace of *Caretta** with two marginals and a vertebral instead of the nuchal scute. This makes fourteen marginals on each side. By joining the opposite marginal sulci, thirteen parallel lines are obtained across the carapace. A middle line is drawn through the carapace, and the modern number of vertebral scutes resulting from a fusion of the fourteen primitive vertebrals is obtained by drawing a series of trapezia. The first of these begins on the first sulcus and ends on the third, with its long axis along the median line and its short axis along the second sulcus. Six trapezia are thus obtained, of which one is in the pygal region and is discarded, while the other, together with two marginals, covers the nuchal and forms a single united scute, leaving four vertebrals, thirteen marginals, and five costals. This is the minimum scutation for *Caretta*, which shows numerous variations to the earlier stages, but never produces any individuals with four costal shields on each side, as it never reached this stage of reduction.

The sulci of the "armadillo" stage in any scuted Testudinate may be determined by drawing lines parallel to the pygal scute, *i.e.*, by continuing the anterior boundary of the last vertebral and on to the anterior boundary of the costal scute of the opposite side. This process repeated for all the costals gives the lines of flexure possessed by the animal when in its "armadillo" stage.

The sulci, or lines of flexure, of the "armadillo" stage persisted in various ways in modern Thecophora.

(1) The number of marginal scutes always equals the number of marginal plates.

(2) The plastron and, at times, the carapace of many forms show movable lobes hinged along former lines of flexure. These lobes are now used for a different purpose, and are compressible, while the presence of the hinges are more a case of secondary reversal than a direct survival of the former condition, as some forms develop the hinged condition late in life (see appended list of hinge-lobed forms).

(3) The plastra of Testudinata are usually concave, except in ovigerous or obese specimens, whereas the normal ventral outline in reptiles is convex.

(4) The plastron is smaller than the carapace, yet, even so, in order to enable the larger carapace to thoroughly encompass it, the plastron has more divisions than the carapace, to form as small a roll as possible when the animal coils up.

(5) The scutes differentiate out long before the formation of marginal bones or endoskeletal expansions in the embryos of modern Thecophora. This shows that the rolling-up habit commenced soon after the Thecophora became terrestrial, and appears to denote that the skin thickened before the endoskeleton expanded. Probably at this stage the scutes overlapped to some extent as they do in the adolescent *Eretmochelys imbricata*, while most modern Thecophora show marginal scutes with imbricate outer edges, and the young when a few weeks old show faintly imbricate scutes.

* The carapace of *Caretta* is used to derive the ancestral type of Thecophoran shown in fig. 5 (Pl. II.).

(6) Transverse bands of pigment run *from marginal to marginal along the sulci* of the carapace, but never across the scutes. Such bands *might betoken* former lines of flexure. The best instance is in *Chrysemys picta.*

(7) As seen from the marginals of *Caretta*, there were probably thirteen sulci, which became reduced by fusion of the divisions. Three lines of flexure was the minimum necessary for coiling up. Most forms developed a stiff ossified corselet some time after attaining this three-groove stage, thereby enabling the condition to become stable.

These modern forms rarely throw back to the four- or five-groove stage, and the appearance of more than four costal scutes on a side is very rare. One form, *Caretta*, stiffened up just before reaching this stage; hence its lines of flexure are not stable, and throwbacks to the stages where the lines of flexure were more numerous frequently occur. Its rapid ossification did not permit it to reach the three-groove stage, but stiffened its corselet even before the four-groove stage had existed very long. Hence the four-groove stage is by no means constant, and the animal, which has a minimum of five costals on each side, throws back to the eight or even nine costals a side stage. To-day this form is the earliest of the Cheloniidæ to complete its ossification, and when on land its ossification must have been correspondingly faster than that of the others. Further proof that the animal developed a stiff plastron before it reached the four-costal stage is that the costal variations are always in excess of five scutes, never four or less.

THECOPHORA WITH HINGED PLASTRA FROM DITMARS.

Superfamily PLEURODIRA.

Family PELOMEDUSIDÆ.

Genus *Sternothœrus*, hinged front lobe.

Superfamily CRYPTODIRA.

Family DERMATEMYDIDÆ.

Genus *Saurotogpus*, front lobe.

Family CINOSTERNIDÆ.

Genus *Aromochelys* } fixed median bridge with anterior
Genus *Cinosternum* } and posterior lobes movable.

Family TESTUDINIDÆ.

Genus *Chrysemys*, colour marks of flexure lines.
Genus *Emys*, hinged at middle.
Genus *Cistudo*, hinged.
Genus *Cyclemys*, hinged at middle.
Genus *Cinyxis*, posterior of *carapace* hinged.
Genus *Notochelys*, hinged.

At varying intervals representatives of the Thecophora became aquatic and underwent secondary changes. The limbs became paddle-shaped, the corselet depressed, the scutes and scales vanished, and ossification was retarded and even repressed, as seen in the Trionychoidea, where the fossil *Pseudotrionyx* has the nuchal, pygal, and an almost complete set of marginals; while *Emyda ceylonensis* has lost the pygal and most of the marginals (Pl. II. fig. 7), until *Aspidonectes spinifer* has only the nuchal left of the dermal bones. Prior to extensive osseous reduction the scutes and scales disappear, although at times the young may show them as rudiments, as in the case of *Carettochelys*, where osseous reduction has not yet commenced.

Some fossil forms, such as *Archelon ischyros* (Pl. III. fig. 2), appear to have taken to water before the Thecophoran platelets were entirely replaced by endoskeletal expansions, which were at an early stage of development, and possibly suffered reduction on the animal taking to the water. The theory arose that this was an ancestral Athecan, reducing its endoskeletal expansions and commencing to develop dermal platelets as proliferations of the marginals. This theory fails to explain why, when in the water, the marginals should increase while the remaining osseous structures were being reduced. It does not explain the origin of the marginals, and does not consider why modern aquatic Thecophora have not progressed toward evolving more dermal platelets by a "proliferation of the marginals" and made an advance on the stages seen in the fossils. Instead of increasing, these platelets have in all cases disappeared, leaving bare the modern Thecophoran carapace, which in several instances shows no greater ossification than that seen in fossils provided with platelets. Palæontology shows that the dermal platelets vanished in the Thecophora, while in *Dermochelys* the ossified scales are disappearing similarly, the fossil Athecans showing a slight ventral reduction while modern *Dermochelys* shows a great reduction, and at times an entire absence, of the ventral armature. This theory also overlooks the highly primitive anatomical features of *Dermochelys*. It is true that this form does present several secondary modifications; yet no animal which can boast of such a pedigree has not undergone similar alterations. Considering the length of time *Dermochelys* has remained in water, it is no matter for surprise that externally it is so far ahead of the Thecophora in aquatic adaptation. It is also well known that, owing to the uniform character of a water environment, the anatomy of an aquatic animal changes more slowly than a similar terrestrial form, although the external shape alters comparatively soon to enable progress through water. Hence it will be seen, especially after perusal of the numerous primitive characters of *Dermochelys* given towards the end of this paper, that this form is the earliest split off from the primitive Testudinate trunk now existing.

After considering the changes brought about by an aquatic life, it is necessary to turn to the terrestrial. These changes are: (1) Disappearance of the temporal roof from the skull by posterior emargination; (2) the head, neck, limbs, and tail become completely and swiftly retractile; (3) there is a tendancy to speedy ossification and fusion of the bony parts; (4) squeezing-out of the neural and pygal plates by the expanding costals; (5) the carapace becomes tectiform, or dome-shaped, to store a greater amount of peritoneal fluid, which acts as a buffer to regulate changes in external temperature and holds a water-supply, while the shape prevents carnivores getting their jaws over the margin of the corselet; (6) the limbs are rounded and columnar; (7) the beaks show serrate margins and strong alveolar ridges on the upper one; (8) retention of claws, scutes, and lepidosis. In view of these characteristics, it would seem that the systematic positions of the Pleurodira and Trionychoidea require considering. The Pleurodira show the most advanced ossification known to the Thecophora in having the pelvis fused to the corselet, the skull greatly modified, and the neural plates squeezed completely out by the costals. This would denote that they had a prolonged terrestrial existence—longer than any of the other living Thecophora—in order to come by the modifications. As all living Pleurodira are amphibious or aquatic, they appear to have taken to water at a recent date, as their aquatic modifications are not very conspicuous. The Trionychoidea appear next in the length of time spent on land. The skull is highly modified, and the pygals and many of the neural plates have been squeezed out by the costals. They also appear to have remained in the water longer than any other Thecophora, seeing that they have lost scutes, scales, and most of their marginal platelets. The claws have also begun to disappear; but this process is delayed, owing to the frictional stimulus they receive when the animals come ashore, as they do at frequent intervals,

to bask by day or to forage at night. Moreover, their corselet is more depressed than in any of the other aquatic Thecophora, which are all following in their wake.

Very similar in external appearance, even to the tubate snout and raised eyes, which are an adaptation to a freshwater environment, is *Carettochelys insculpta* Ramsay, figured in de Rooij, known only from New Guinea. It is covered with smooth skin, except for a row of four rudimentary scales on the front edge of each arm and a row of broad dorsal scales on the tail. The limbs in this animal, which is probably essentially a swimming form, are modified into short paddles with two claws each. Ossification is very pronounced, and even in the very young the marginals and plastral bones are well developed. The skull has a wide quadrato-temporal arcade, while the neural plates of the carapace are separated from each other in the adult by the costals, which are beginning to squeeze them out, as they have already done in the Pleurodira. The young usually have the neurals contiguous, and it is only when the costals expand in the adult that they are separated. Apart from this, the young show a few rudimentary vertebral scutes anteriorly which disappear later. This form appears to be a Pleurodiran, which took to water before the neurals were entirely squeezed out, but it remained on land long enough to commence this alteration. Its strong ossification also denotes a prolonged terrestrial stay, while the period spent in water is considerably less than that spent by the Trionychoidea, as it has retained its ossification, which is unretarded, while some scales still remain, and the vertebral scutes still appear on the young.

The Cheloniidæ appear to have left the marsh for dry land after the Trionychoidea took to water. Their terrestrial life was too brief to have a marked effect on their skulls or inframarginal scutes, and then they become aquatic. Their aquatic life has been far shorter than that of the Trionychoidea, as they still retain scutes, scales, and marginals, while the corselet, although depressed, is not as depressed as in the Trionychoidea. The reduction of claws to two or one and the formation of elongate paddle-like limbs appear to be due to almost continuous progression through strong waves and currents, for, as they rarely come ashore, their claws do not receive the frictional stimulus necessary for their maintenance.

The Chelydridæ also appear to have left the marsh recently, and, as seen from the skull, spent a short time on land, probably somewhat longer than the Cheloniidæ, but not sufficiently to lose their inframarginal scutes or caudal ossicles. They then took to water, where they have not remained sufficiently long to enable them to lose their scutes, claws, or marginal bones.

As no paper on Testudinate evolution is complete without a reference to that rare form, the leathery turtle, *Dermochelys coriacea* (Linné), a short description of this animal will not be out of place. For a detailed description the reader is referred to 'Testudinata of Ceylon: Spolia Zeylanica,' Sec. B. 1930, by the writer.

Dermochelys coriacea is the sole living representative of the Atheca. It is a deep-water form, and only comes into littoral waters prior to coming ashore to deposit its spherical soft-shelled eggs, of which about 130 are laid at a time. The young on hatching betake themselves to deep water, and the intermediate stages are not known. During development the first pigment to appear on the hyaline embryo is the dark eyes and longitudinal streaks of white pigment, which extend over the neck and corselet. On hatching, the animal is a slaty black, with seven longitudinal white bands dorsally and five ventrally. The entire carapace and plastron are broken up into numerous lizard-like subequal scales, except for the white lines, which consist of rows of somewhat larger scales in a single row (for figure, see de Rooij). The limbs at times show rudimentary claws, and the fore flippers of a specimen, which had no claws on hatching, show two well-developed claws on each after its death, 12 days later.

The corselet scales ossify with age, and their boundaries disappear as do the claws, and the entire animal is covered with smooth skin. The single rows of enlarged scale shows up as a series of knobs where the carinæ of the scales project above the intervening smaller scales, which are flat. The white pigment disappears, being broken up into dots, which persist longest on the neck. Throughout life the skeleton of the animal retains its embryonic proportions, except the hyoplastra and hypoplastra, which elongate to overlap at the mid-ventral line, whereas in tl e embryo they ended away from this region, which was the line of flexure over the yolk. The plastral bones have no entoplastron—probably lost as a result of the strong arm-action of this fast-swimming form, which can swim and dive easily as soon as hatched, whereas the Cheloniidæ usually float at the surface for 48 hours, buoyed up by the internal yolk material, and are unable to dive with any facility for the first week or more.

Some noteworthy features of *Dermochelys* are the following, of which the primitive ones are denoted by an asterisk :—

(1)* Young covered in lizard-like, small scales; those on head enlarged as in many lizards; scales on neck and limbs subequal, not differentiated into large and small as in the Thecophora; *corselet scaly.*

(2) Adult loses all scale boundaries and is covered with smooth skin, probably to lessen friction in a fast-swimming pelagic form.

(3) The ventral osseous platelets of the adult have sharper carinæ than the dorsal ones, showing that the animal is not a recent departure from land, where friction would have evolved smooth platelets as in the Caiman.

(4)* Beaks with smooth edges; no alveolar ridges.

(5) In the Testudinata the eye is oblique; this form shows an exaggeration of this angle.

(6)* A greater number of corselet ridges than the Thecophora, which usually show a few ridges, especially when young.

(7)* There is a lizard-like dorsal cutaneous crest to tail.

(8)* The skeleton does not advance in development, but remains in the embryonic condition and resembles the skeleton of embryonic or very young Thecophora.

(9)* The nuchal bone is free, and is ventrally attached to the dermal carapace, as is the case in some young Thecophora, especially *Emyda ceylonensis.*

(10)* The skull is palæorbital, and has the temporal region completely roofed over; it has no parietal buttresses. A large parasphenoid bone nearly separates the pterygoids.

(11)* Sigmoid flexure of neck is the least marked of the whole order.

(12)* The pelvis is very primitive. If it were completely ossified, Nopcsa says "it would recall the most primitive reptilian pelvis. It would be more primitive than the pelvis of the Amphichelydæ."

(13)* The corselet ossification is in its pristine condition, whereas the Thecophora have progressed two stages further.

(14) Entoplastron lost owing to strong arm action in this pelagic form.

(15) External shape shows the highest Testudinate evolution for an aquatic life. It has reached the short torpedo-like shape with perfect streamlining, the anterior end being wider than the posterior, which, owing its tapering form, does not create a vacuum in the water behind, to retard the progress of the animal.

(16)* Several eggs in a nest produce perfect double embryos, a very rare occurrence in the Thecophora.

(17)* There are several Thecophora covered in smooth skin like *Dermochelys*, but none possess young or embryos with a scaly corselet. As all

reptiles are scaly, the ancestral Testudinate type must have been likewise.

(18) The embryos of *Dermochelys* never show the large-corselet scutes of the Thecophora which appear in the latter prior to pigmentation.

(19)* The white longitudinal bands and the eye pigment are the first colours to appear in the hyaline 27-day-old *Dermochelys* embryo. Probably the ancestral form had large scales, similar to those on the carapace ridges, continued along the white pigment of the neck. Subsequently these scales disappeared when the telescoping neck developed, and only the pigment remained.

The following conclusions are to be drawn from this paper on Testudinata :—

(1) The nuchal bone is an anchor for retractile neck-muscles.

(2) There are two types of skull; the original form had the temporal region roofed over. This roof was lost when the animal came ashore and the secondary type arose. The comparative period spent on land can be ascertained by the amount of change undergone by the temporal roof.

(3) The primitive Testudinate was a marsh dweller which was covered with scales. It was more or less lizard-like, and the lateral dermal folds formed the margins of the future carapace.

(4) The pectoral girdle shifted anteriorly over the ribs to avoid constriction between them and the dermal corselet, and then sent out osseous processes to stabilise its position. The scapula is still external to the ribs, and its distal end is in contact with the nuchal fold of the carapace.

(5) One branch took to water, the rest came ashore, where they remained for short or long periods before taking to water. Marsh-land water is the order of change of habitation in Thecophora.

(6) During the terrestrial period they first protected themselves by rolling up like armadillos, and this habit broke up the corselet skin into scutes.

(7) Later the corselet ossified, and complete retraction into the corselet was substituted for coiling up.

(8) Dermochelys is the result of the first division of the Testudinata, and, as it remained in water, retained many primitive characters the others lost during their terrestrial period.

(9) There are two sets of dermal platelets—an upper Athecan one of ossified scales and a lower Thecophoran layer. The first has disappeared entirely from modern Thecophora, which still retain a few remnants of the second layer.

(10) By employing an ellipse with fourteen marginals, the carapace scutes of *Caretta* can be drawn out geometrically together with its latest variations.

Works of Reference.

1. Parker, W. K. 1868. A Monograph on the Structure and Development of the Shoulder-girdle and Sternum in Vertebrates. Ray. Soc. Monograph.

2. ——— 1880. Embryology of Green Turtle. 'Challenger' Reports, vol. i. pt. 5.

3. Woodward, A. Smith. 1887. Leathery Turtles Recent and Fossil. Proc. Geol. Assoc. vol. x. pp. 2–14.

4. Haycroft, J. B. 1890. Development of Carapace in Chelonia. Trans. Roy. Soc. Edinburgh, vol. xxxvi.

5. Cope, E. D. 1896. Ancestry of Testudinata. Amer. Nat. vol. xxx.

6. Hay, O. P. 1897. Protostega, the Systematic Position of *Dermochelys* and the Morphogeny of the Chelonian Carapace and Plastron. Amer. Nat. vol. xxxii

7. Goette, A. 1899. Entwicklung des knochen Rückenschildes der Schildkroten. Zeitschrift fur wiss., Zool. vol. lxvi. pp. 407–434.
8. Dollo, L. 1901. Sur l'Origine de la tortue Luth, *D. coriacea*. Bull. Soc. Roy. Sci. Med. Nat. Bruxelles.
9. von Zittel, K. A. 1902. Text-book of Palæontology, vol. ii.
10. Burne, R. H. 1905. Notes on Muscular and Visceral Anatomy of *Dermochelys coriacea*. Proc. Zool. Soc. Lond. pp. 291–324.
11. Newman, H. H. 1906. Significance of Scute and Plate Abnormalities in Chelonia. Biological Bull. vol. x.
12. Hay, O. P. 1908. Fossil Turtles of N. America. Carn. Inst. Wash.
13. Wieland, G. R. 1909. Revision of the Protostegidæ. Amer. Journ. Sci. (4) vol. xxvii.
14. Veeluys, J. 1913. Phylogeny of the Carapace and on the Affinities of the Leathery Turtle, *D. coriacea*. Report of 83rd Meeting of Brit. Assn. for Adv. of Sci, Birmingham, pp. 791–807.
15. Watson, D. M. S. 1914. *Eunotosaurus africanus* Seeley, and the Ancestors of Chelonia. Proc. Zool. Soc. Lond. pt. 2.
16. de Rooij, N. 1915. Reptiles of the Indo-Australian Archipelago, Leiden.
17. Hay, O. P. 1921–22. Phylogeny of Shell of Testudinata and Relationships of *Dermochelys*. Journ. Morph. Phil. vol. xxxvi
18. Nopcsa, F. 1923. Reversible and Irreversible Evolution in Reptiles. Proc. Zool. Soc. Lond. pt. 2.
19. ——— 1923. Die Familien der Reptilien. Berlin.
20. ——— Heredity and Evolution. Proc. Zool Soc. Lond pp. 633–665.
21. Ditmars. 1927. Reptiles of the World.
22. Nopcsa, F. 1928 Genera of Reptiles. Palæobiologica.
23. Ruckes, H. 1929. Studies in Chelonian Osteology, Pt. II. Ann. N. York Acad. Sci. vol. xxxi. pp. 81–120.

EXPLANATION OF THE PLATES.

Plate I.

Stages of corselet ossification.

Fig. 1. *Dermochelys* with Othecan platelets in white and narrow plastral bones. Skull palæorbital. Nuchal cross-hatched.
2. Reconstruction from fossils. Athecan platelets white, Thecophoran platelets black, and endoskeletal expansions commencing
3. Thecophoran. Total loss of Athecan platelets. Skull neo-orbital and emarginate. Curving neck. Expansions from endoskeletal and plastral bones.

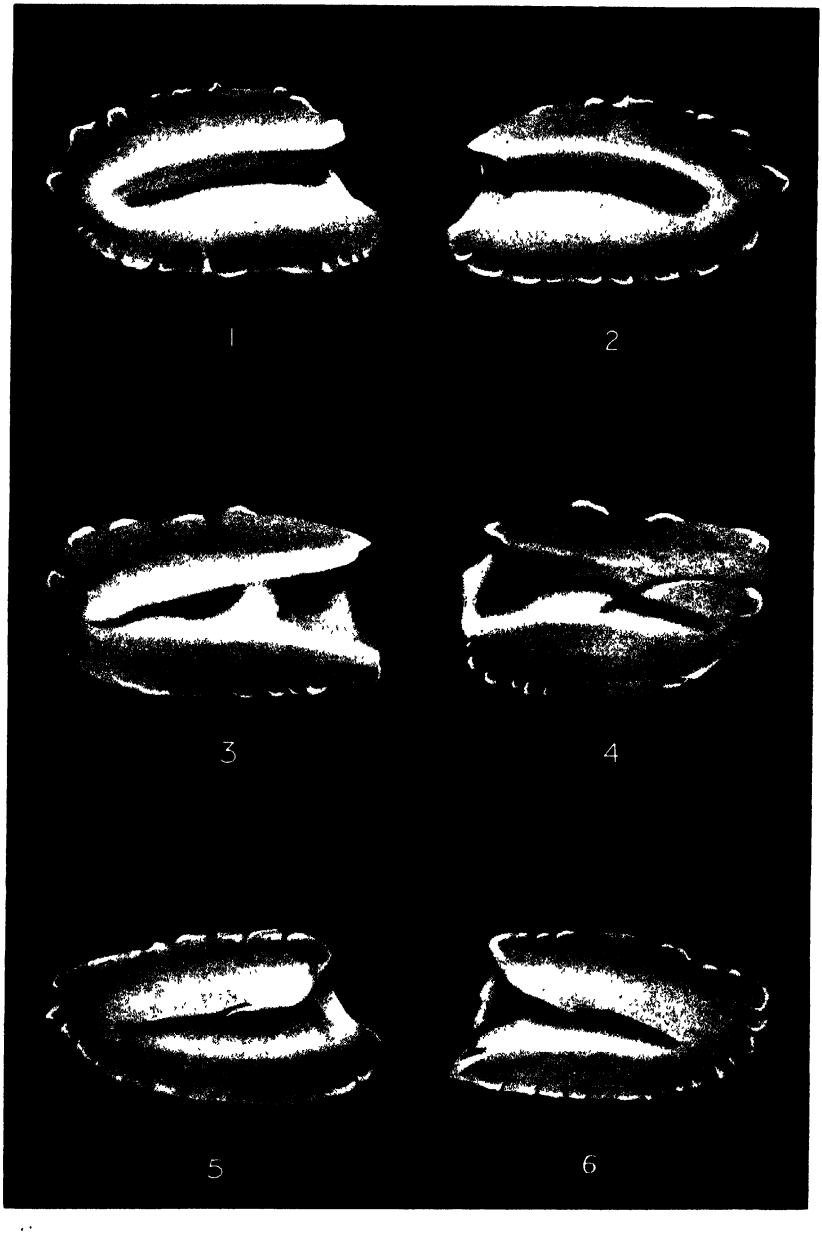
Plate II.

Evolutionary sequence.

Fig. 1. Lizard-like marsh dweller. Scaly covering. Nuchal scales denoted by arrow.
2. Formation of nuchal fold and shifting of nuchal scales under it
3. Corselet extends posteriorly Scales at base of neck and limbs lost through friction.
4. Thecophoran platelets in black.
5. Derivation of ancestral Thecophoran from carapace of *Caretta* with 14 marginals. Thecophoran platelets shown in black.
6. Nuchal scute of *Caretta caretta* (Linné) divided into two marginals and a vertebral (dotted lines).
6A. *Caretta* showing fusion of scutes. Thecophoran platelets black.
7. *Emyda granosa ceylonense* (Kelaart), showing loss of scutes, scales, and most of Thecophoran platelets.

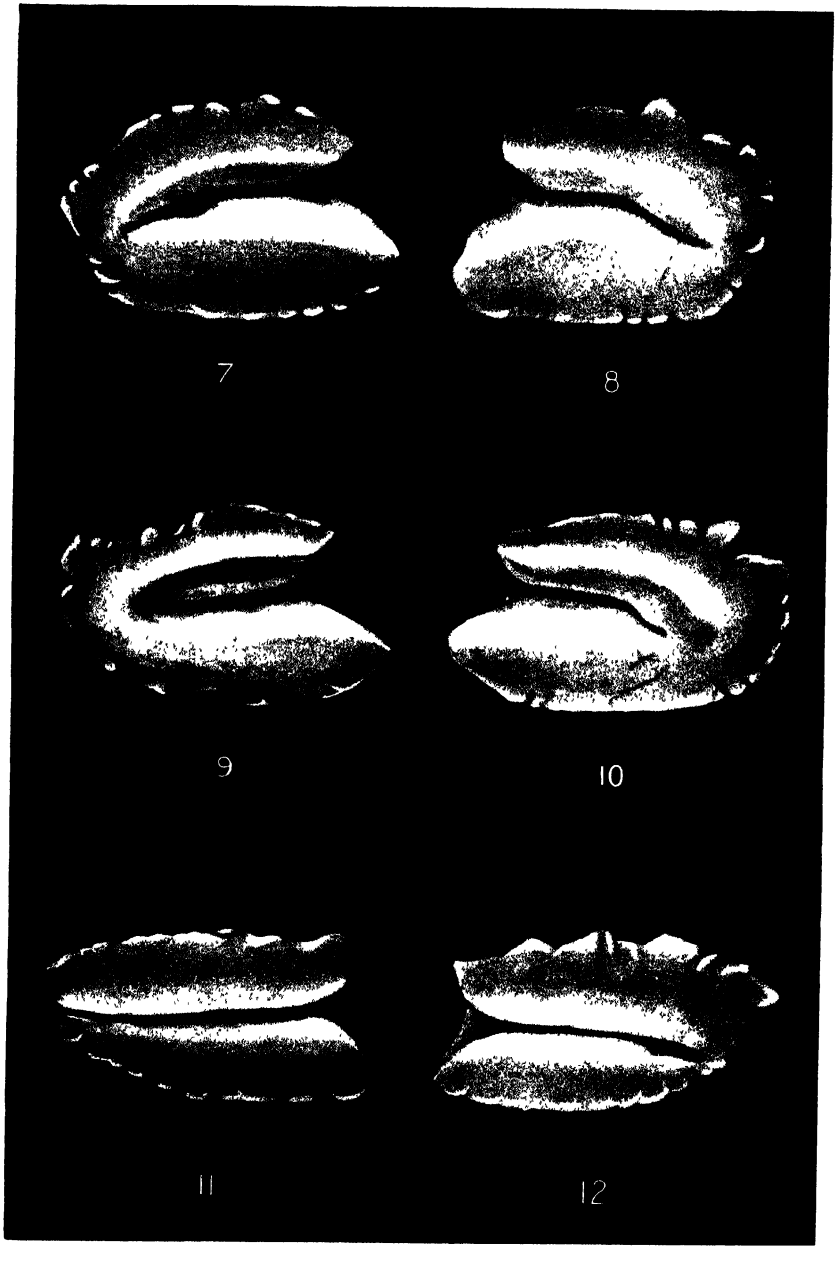
Plate III.

Fig. 1. Armadillo-like habit.
2. *Archelon ischyros* Weiland, a fossil showing Thecophoran platelets (black) as supramarginals and epineurals, disappearing before the expanding endoskeletal callosities. Modified from Veeluys.



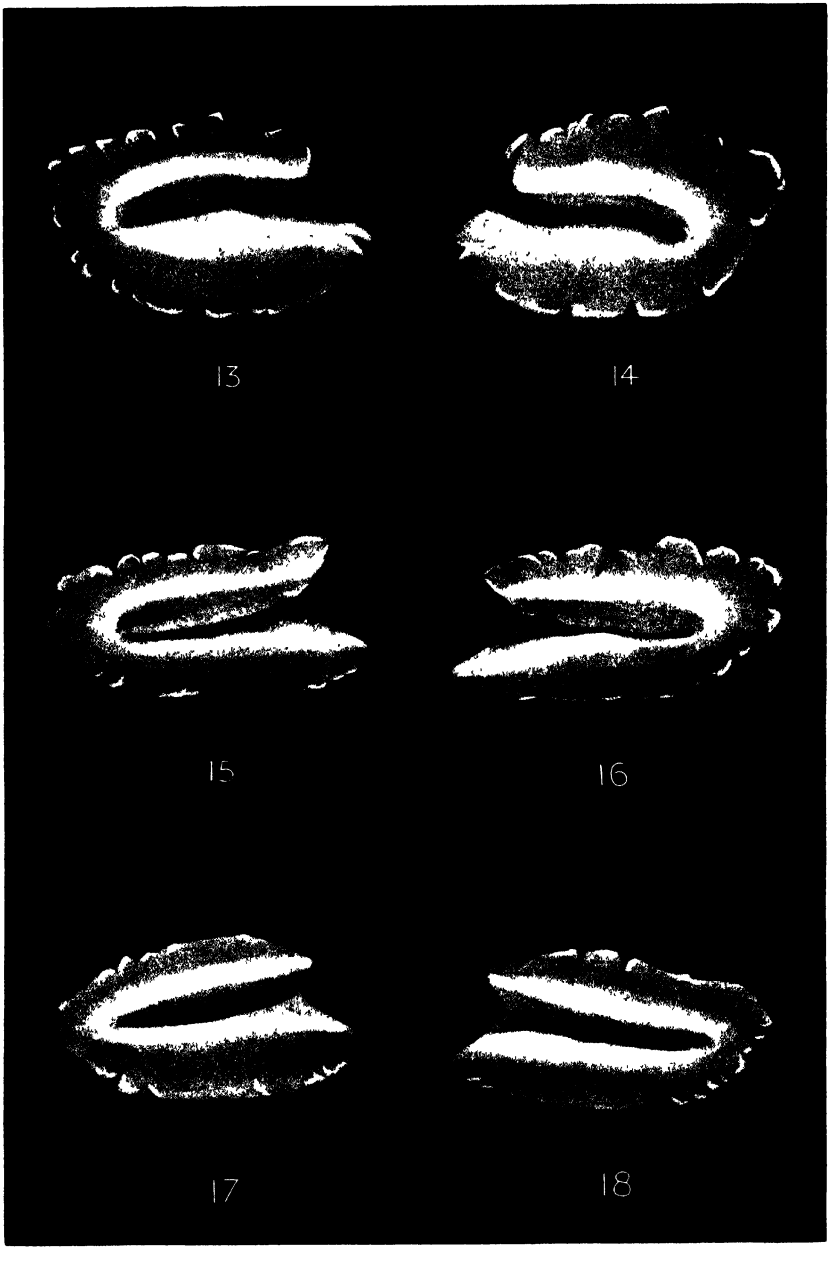
F. Angel, del.

OTOLITHS OF LARGE EELS FROM THE LAKE OF TUNIS.



F. Angel, del.

OTOLITHS OF LARGE EELS FROM THE LAKE OF TUNIS.



F. Angel, del.

OTOLITHS OF LARGE EELS FROM THE LAKE OF TUNIS.



F. Angel, del.

OTOLITHS OF LARGE EELS FROM THE LAKE OF TUNIS.

51. The Otoliths of some Large Eels from the Lake of Tunis.

By Dr. A. Gandolfi Hornyold, F.R.M.S., F.Z.S.

[Received July 9, 1930: Read November 18, 1930.]

(Plates I.–IV.)

Last winter I worked on the eel of the Lake of Tunis at the Oceanographical Station of Salammbô. I chiefly studied the age, growth, and sex of the small Silver Eel, but I also studied the otoliths of 13 large silver females. I most sincerely thank M. and Mme H. Heldt, Director and Assistant of the Station, for all that they have done to help me in my work. My thanks are also due to M. Fernand Angel, of the Muséum National d'Histoire Naturelle of Paris, for the drawings and for the great pains he took to render the otoliths as perfectly as possible, a by no means easy task.

I begin by giving the length and weight of the eels, and the dimensions of their otoliths, as also the magnification:—

Length. cm.	Weight. gr.	Dimensions of otoliths. mm.			mm.	Magnification.
101	1890	Fig. 1.	Left, 5·3 × 3·0	Fig. 2.	Right, 5·3 × 2·9	× 10
100	1780	3.	„ 4·5 × 2·5	4.	„ 4·0 × 2·7	× 14
99	2110	5.	„ 5·3 × 2·9	6.	„ 5·0 × 2·7	× 12
99	1620	7.	„ 5·1 × 3·4	8.	„ 5·0 × 2·7	× 12
96	1675	9.	„ 5·5 × 3·2	10.	„ 5·0 × 3·4	× 11
93	1405	11.	„ 4·9 × 2·5	12.	„ 5·5 × 3·0	× 13
91	1380	13.	„ 5·0 × 3·2	14.	„ 5·0 × 2·5	× 12
90	1035	15.	„ 5·6 × 2·7	16.	„ 5·1 × 3·2	× 11
89	1150	17.	„ 4·8 × 2·5	18.	„ 5·6 × 2·6	× 12
88	1385	19.	„ 5·3 × 3·0	20.	„ 5·0 × 3·1	× 12
85	1210	21.	„ 5·0 × 2·9	22.	„ 5·3 × 2·8	× 12
81	1175	23.	„ 4·1 × 2·4	24.	„ 4·1 × 2·4	× 15
77	775	25.	„ 5·0 × 2·8	26.	„ 5·0 × 2·8	× 12

The table confirms my previous observations, showing that both the saccular otoliths can be of the same size or that they can differ more or less; for instance, the left otolith of the 93-cm. female measures 4·9 × 2·5 mm. and the right otolith 5·5 × 3 mm., the left otolith of the 70-cm. female measures 5·6 × 2·7 mm. and the right otolith 5·1 × 3 mm. Both the otoliths of the 81 and 79-cm. females are of the same size, and measure respectively 4·1 × 2·4 and 5 × 2·8 mm. There are two females measuring 99 cm., and their otoliths measure: left 5·3 × 2·9, right 5 × 2·7 mm., and left 5·1 × 3·4, right 5 × 2·7 mm., which shows that the otoliths of eels of the same size can differ more or less.

The smallest of the 13 females measured 77 mm., and its otoliths measured both 5 × 2·8 mm. and were larger than those of the 100-cm. female, which only measured 4·5 × 2·5 and 4 × 2·7 mm. The table gives various examples, and also shows that the size of the otolith is not in absolute proportion to the length of the eel, though naturally the otoliths of a 50-cm. eel would be smaller than those of a 100-cm. long eel.

The largest female measured 101 cm., with a weight of 1890 gr., and the otoliths measured 5·3 × 3 and 5·3 × 2·9 cm. The heaviest eel measured 99 cm., with a weight of 2110 gr., and the otoliths measured 5·3 × 2·9 and 5 × 2·7 mm. The right otolith of the 83-cm. female had the greatest length, and measured 5·6 × 2·6 mm., but the corresponding left otolith only measured 4·8 × 2·5 mm. The two broadest otoliths were the left otolith of the 99-cm. and 1620-gr eel, which measured 5·1 × 3·4 mm., and the right otolith of the 96-cm. eel, which measured nearly the same, 5 × 3·4 mm.

The left otolith of the 101-cm. eel (Pl. I. fig. 1) is elongated; the dorsal rim is curved, with various indentations, the ventral rim is nearly straight, and the posterior rim forms a rounded protuberance with a slight notch. The antirostrum is fairly large and flattened, and the rostrum is very large and rounded. The excisure is large. The undivided sulcus opens out widely on the dorsal front of rostrum; it is straight and very wide, ending at about five-sixths of the length of the otolith.

The right otolith (Pl. I. fig. 2) is elongated; the dorsal rim is curved, with a few indentations, the ventral rim is straight, and the posterior rim forms a point. The antirostrum is small and forms a sharp point, and the rostrum is fairly large and obtuse. An excisure is present. The straight, wide, undivided sulcus opens out very widely on the dorsal part of rostrum, and ends rounded at about three-fourths of the length of the otolith.

In both these otoliths the deepest part of the sulcus forms a narrow channel, and the sulcus slopes down very gradually on the ventral side and more abruptly on the dorsal side.

The left otolith of the 100-cm. eel (Pl. I. fig. 3) is very elongated; the dorsal rim is very slightly curved, the ventral rim is straight, and the posterior rim is rounded, forming a very slight protuberance in the centre with a small notch above and below. The antirostrum forms a small sharp point, and the rostrum is small and flattened. An excisure is present. The straight undivided sulcus opens out widely on to the frontal rim and tapers down gradually, and ends in a point at about six-sevenths of the length of the otolith. It is crossed by a ridge one-third of its length, and both the opening and the end are deep. The sulcus slopes down gradually on the ventral side.

The left otolith (Pl. I. fig. 4) is much less elongated and narrow; the dorsal rim would lie straight were it not for some irregularities, the ventral rim is very curved, with some indentations near the rostrum, and the posterior rim is flattened and slightly oblique, with a small rounded protuberance in the centre with a large notch above and a smaller below. The antirostrum is small and blunt; the rostrum is flattened, with some indentations on the lower part which continue on the ventral rim. An excisure is present. The straight undivided sulcus opens out widely on to the dorsal side of the rostrum and tapers down gradually, ending rounded at about four-fifths of the length of the otolith. A narrow, curved, fairly deep channel begins in the deepest part of the sulcus, and opens on to the posterior rim in the notch above the protuberance.

The left otolith of the 99-cm. and 2110-gr. eel (Pl. I. fig. 5) is narrow and elongated, the dorsal rim is very slightly curved and indentated, the ventral rim is curved, with a few indentations near the posterior rim, and the posterior rim forms three protuberances. The antirostrum is small, the rostrum is large, and both are rounded. There is a small excisure. The sulcus is undivided and slightly curved, opening widely on dorsal part of rostrum; it tapers down gradually, ending rounded at about three-fourths of the length of the otolith. There is a small fissure on the dorsal side of the sulcus running a short distance towards the frontal rim. The ventral side of the sulcus slopes down very gradually so that the end is not very distinct.

The right otolith (Pl. I. fig. 6) is also elongated and narrow; the dorsal rim is

slightly curved and indentated, the ventral rim is curved and slightly indentated, and the posterior rim forms three protuberances. Both the rostrum and the antirostrum are pointed. An excisure is present. The straight undivided sulcus opens out widely on to the frontal rim and tapers down gradually, ending rounded at about two-thirds of the length of the otolith. There is a slight constriction on the dorsal side of the sulcus at about half the length, but not sufficient to warrant a division in ostium and cauda. The ventral side slopes down gradually, but the end of the sulcus is more distinct than in the left otolith.

The left otolith of the 99-cm. and 1620-gr. eel (Pl. II. fig. 7) is elongated; the dorsal rim is curved, with large indentations, the ventral rim nearly straight, and the posterior rim forms a point. The antirostrum is large and forms a blunt point, and the rostrum is very large and rounded. An excisure is present. The very wide, shallow, slightly curved, and undivided sulcus opens out widely on the frontal rim, and ends rounded at about five-sixths of the length of the otolith. The sulcus slopes down on the ventral side, and the deep part is very narrow.

The left otolith (Pl. II. fig. 8) is less elongated; both the dorsal and ventral rims are slightly curved and the posterior rim is rounded. All the rims are more or less indentated, and the posterior rim has a large protuberance. The antirostrum is barely indicated and the rostrum is very large; both are obtuse. An excisure is indicated. The very wide, shallow, curved, undivided sulcus ends rounded at about five-sixths of the length of the otolith. The sulcus opens widely on the frontal rim, and is more curved than is the case in the left otolith. It is even more shallow, sloping down very gradually on to the ventral side, so that the end is not very distinct.

The left otolith of the 96-cm. eel (Pl. II. fig. 9) is elongated; the dorsal rim is curved, with very large and deep indentations towards the posterior rim, giving an impression as if part of the otolith had been eaten or broken away. The ventral rim is curved and the posterior rim is rounded, with a large notch. Both the antirostrum and the rostrum are large, forming sharp points, and the excisure is very large, forming a right angle with the antirostrum and rostrum. The wide, straight, undivided sulcus opens out widely on the frontal rim, and ends rounded at about three-fourths of the length of the otolith. The sulcus is deeper than in some of the previously described otoliths, and the end is more distinct.

The right otolith (Pl. II. fig. 10) is elongated; both the dorsal and ventral rims are curved and the posterior rim is rounded. The dorsal and posterior rims have large indentations, and the ventral rim has only a few slight ones near the rostrum. The wide, straight, undivided sulcus opens out widely on the frontal rim and ends rounded at about three-fourths of the length of the otolith, tapering down on the dorsal side near the end. The ventral side slopes down very gradually near the opening, so that the form of the sulcus is not very distinct, but it becomes more so near the end.

The left otolith of the 93-cm. eel (Pl II. fig. 11) is very elongated; the dorsal rim is very slightly curved, the ventral rim is straight for about half the length of the otolith and oblique till the posterior rim. The posterior rim forms a blunt point with a small protuberance below separated by a notch. The rims have very slight indentations. The antirostrum and rostrum are large and obtuse. An excisure is present. The oblique, narrow, undivided sulcus opens out on the dorsal side of the rostrum and ends on the notch on the posterior rim.

The right otolith (Pl. II. fig. 12) is less elongated; the dorsal and ventral rims are curved and the posterior rim ends in a point. The dorsal rim is serrated nearly all along, and there are indentations on the posterior and a smaller one on the ventral rim. The antirostrum is fairly large and forms a sharp point, and the rostrum is comparatively small and blunt. An excisure is present. The sulcus is narrow, but wider than in the left otolith, opening widely on to the frontal rim, covering the greater part of it, then tapers down, becomes narrow, and ends rounded near the

posterior rim. Like the left otolith it is undivided, but it is curved and slightly oblique.

The left otolith of the 91-cm. eel (Pl. III. fig. 13) is elongated; the dorsal and ventral rims are curved and the posterior rim is rounded. Both the dorsal and posterior rims are serrated, and there are two slight indentations on the ventral side of the rostrum. There is neither antirostrum nor excisure, and the rostrum is very large and obtuse, the indentation giving it a slightly irregular aspect. The sulcus is undivided, very wide and straight, with an opening covering the greater part of the frontal rim, ending rounded at about three-fourths of the length of the otolith. On the ventral side the sulcus is very shallow, sloping down gradually, but the contour is fairly distinct.

The right otolith (Pl. III. fig. 14) is elongated; the dorsal rim is curved and serrated, the ventral rim is also curved, and the posterior rim is rounded. The antirostrum forms a small protuberance, the rostrum is large and forms a blunt point, and an excisure is present. The sulcus is very wide, undivided and slightly curved, ending at about three-fourths of the length of the otolith, and, as in the left otolith, the opening covers the greater part of the frontal rim.

The left otolith of the 90-cm. eel (Pl. III. fig. 15) is very elongated; the dorsal rim is slightly curved, with large indentations, the ventral rim is curved, and the posterior rim is much indentated, ending in a protuberance. Both the antirostrum and rostrum are very large and form blunt points. The excisure is large and forms a right angle between them. The sulcus straight, very shallow, wide, and opens very widely on to the frontal rim, ending rounded at about three-fourths of the length of the otolith.

The left otolith (Pl. III. fig. 16) is even more narrow and elongated; the dorsal and ventral rims are slightly curved and the posterior rim is rounded. Both the dorsal and posterior rims are serrated. Both the rostrum and antirostrum are large and very pointed. The excisure is very large, forming a right angle between them as in the left otolith. The sulcus opens out very widely on to the frontal rim, covering the greater part of it; it is undivided, straight, and ends rounded at about three-fourths of the length of the otolith. The ventral side is very shallow, so that the end is not very distinct.

The left otolith of the 89-cm. eel (Pl. III. fig. 17) is elongated; both the dorsal and ventral rims are curved and the posterior is flattened, with three small protuberances. There are a few indentations on the dorsal and ventral rims. The antirostrum is small and very pointed; the rostrum is large, and forms a blunt point. The excisure is large, and forms a right angle between the rostrum and the antirostrum. The sulcus opens out fairly widely on to the frontal rim; it is straight, undivided, shallow, and ends in a point near to the posterior rim.

The right otolith is more elongated (Pl. III. fig. 18), and the form is very similar to that of fig. 15 (Pl. III.), which represents the left otolith of the 90-cm. eel. Both the dorsal and ventral rims are slightly curved, and the posterior rim ends in two small protuberances and has various indentations. The dorsal and ventral rims have also a few indentations. The antirostrum is large and forms a blunt point, the rostrum is also very large, forming a blunt point, and the excisure forms a right angle between them. The long, straight, undivided sulcus opens out widely on to the frontal rim; it is very shallow, and ends rounded near the posterior rim, but a little further off than in the left otolith. Owing to its shallowness the end is not very sharply defined.

The left otolith of the 88-cm. eel (Pl. III. fig. 19) is elongated; the dorsal and ventral rims are very curved and the posterior rim ends in a point. There are small indentations on all the rims, and a deep notch on the dorsal rim. The antirostrum and rostrum are large, the first sharply pointed and the second rounded, and the excisure forms a right angle between them. The wide, undivided, slightly oblique sulcus opens out on to the dorsal side of the rostrum, ending rounded at

about three-fourths of the length of the otolith. The sulcus is very shallow, especially on the ventral side, and the end is not very distinct.

The right otolith (Pl. IV. fig. 20) is elongated; both dorsal and ventral rims are very curved; the dorsal rim has a deep notch, and the posterior rim is rounded, with slight indentations. Both the rostrum and the antirostrum are large and obtuse. The excisure forms an angle of 75° between them. The wide, straight, shallow, undivided sulcus opens out on to the dorsal side of the rostrum fairly widely, ending rounded at about two-thirds of the length of the otolith. The ventral side of the sulcus is very shallow and the form is not very sharply defined.

The left otolith of the 85-cm. eel (Pl. IV. fig. 21) is elongated; both the dorsal and ventral rims are curved and the posterior rim ends in a protuberance. The antirostrum is large and forms a sharp point with a notch below, the rostrum is large and flattened, and the excisure forms a right angle between them. The sulcus is narrow, oblique, opening out not very widely on to the dorsal side of the rostrum and ending in a point quite close to the posterior rim; the ventral side is shorter, and the contour is indistinct just after the opening, till two-thirds of the length, then becoming deeper, gradually tapering till near the end when there is a constriction, and the sulcus becomes quite fine. It is not divided into ostium and cauda.

The right otolith (Pl. IV. fig. 22) is elongated; both the dorsal and ventral rims are curved and the posterior ends in a protuberance. All the rims have slight indentations. The antirostrum is flattened and divided by a notch, the rostrum is large and pointed, and the excisure forms a right angle between them. The narrow, curved, undivided, oblique sulcus opens out widely on to the frontal rim, covering the greater part of it; it tapers down soon after opening, becoming very narrow, and ends on the posterior rim not very distinctly.

The left otolith of the 81-cm. eel (Pl. IV. fig. 23) is elongated; both the dorsal and ventral rims are curved, and the posterior rim ends in a flattened protuberance with a notch above and a slight one below. The antirostrum is small and flattened, and the rostrum is very large and obtuse. An excisure is present, and the antirostrum and rostrum form an angle of about 130°. The wide, straight, undivided sulcus opens out very widely on to the frontal rim, covering the greater part of it, and ends rounded at about five-sixths of the length of the otolith. The ventral side of the sulcus is very shallow, sloping down very gradually so that the contour is not very distinct.

The right otolith (Pl. IV. fig. 24) is elongated; both the dorsal and ventral rims are curved, and the posterior rim is rounded, with a small point above the centre. The dorsal and ventral rims have some slight indentations. The antirostrum is very small and rounded, and the rostrum is large and obtuse. The excisure is very large, forming an angle of about 125° with the antirostrum and rostrum. The wide, straight, undivided sulcus opens out very largely on to the frontal rim, and ends rounded at about five-sixths of the length of the otolith. The ventral side of the sulcus is very shallow, and the contour is not always distinct.

The left otolith of the 77-cm. eel (Pl. IV. fig. 25) is elongated; both the dorsal and ventral rims are curved, with slight indentations. The posterior rim ends in a protuberance. The antirostrum is large and pointed, and the rostrum is large and obtuse. An excisure is present, forming an angle of about 80° between them. The wide, undivided, slightly undivided sulcus opens on to the dorsal side of the rostrum, and ends rounded close to the posterior rim. The ventral side of the sulcus is very shallow and the contour not very distinct.

The right otolith (Pl. IV. fig. 26) is less elongated; both the dorsal and ventral rims are curved and the posterior rim is rounded. Both the dorsal and posterior rims are serrated and the ventral has practically no indentations. The excisure forms nearly a right angle between the antirostrum and the rostrum. The very wide, nearly straight, undivided sulcus opens out widely on to the frontal rim, and

ends rounded at about three-fourths of the length of the otolith. Owing to the shallowness of the ventral side of the sulcus, part of the contour is not distinct.

There seems to be in some cases a certain likeness in the irregularities in both otoliths, such as that of the notch on the antirostrum or in the form, such as in figs. 5 and 6 and 15 and 16 (Pls. I. & III.), which represent the otoliths of the 99-cm. and 2110-gr. and 90-cm. eels. By comparing the figures it is easy to find various other examples.

Mr. G. Allan Frost found that some otoliths of large eels had a distinctly clupeoid type, and the drawings of many of the otoliths correspond to his description of the clupeoid type (Pls. I.–IV. figs. 1, 2, 7, 9, 10, 15, 16, 17, 18, 19, 20, 21, 25, and 26). Rostrum, antirostrum, and excisure present, the sulcus wide and open, undivided or with a slight angle of lower line.

It is, as far as I know, the first time that otoliths of the eel (*Anguilla vulgaris* Turton) from Northern Africa have been described, and I think that this paper proves that their otoliths show as much variation as do those of the eel in European waters.

Mr. G. A. Frost, F.Z.S., who kindly initiated me into the morphological study of the otoliths, gives the following description of the otolith of the adult eel :—

"In the adult eel the form is elongated, the dorsal rim curved or straight, the ventral rim is slightly curved, the posterior rim is usually pointed, and the front consists of a rostrum, antirostrum, and an excisure. The sulcus opens widely on to the frontal rim, and the cauda, which is usually narrow, may be curved or straight. In some cases the sulcus widens out, and is not divided into ostium and cauda. The sulcus does not reach the posterior rim."

There is considerable differentiation in the form presented in the otolith of adult eels. The utricular and lagænar otoliths are very small in comparison with the sagitta.

In comparing the figures of the 26 otoliths belonging to 13 Silver female Eels from 77–101 cm. long, we can observe a very considerable differentiation in their form or in that of the sulcus, or in both. The normal type is rare, and in none of the otoliths is the sulcus divided into an ostium and cauda. No two otoliths of the same eel are identical, but all have greater or lesser differences in the form or in that of the sulcus, or in both. I only give a few examples.

The left and right otoliths of the 101-cm. eel are similar, but in the left otolith the antirostrum is flattened, the rostrum rounded, and the posterior rim forms a rounded protuberance. In the left otolith the antirostrum forms a sharp point, the rostrum is obtuse, and the posterior rim forms a point. (Pl. I. figs. 1 & 2.)

The otoliths of the 99-cm. and 1620-gr. eel offer another example. In the left otolith the antirostrum forms a blunt point, the rostrum is rounded, and the posterior rim forms a point. In the right otolith the rostrum is barely indicated, the rostrum obtuse, and the posterior rim is rounded. In the right otolith the sulcus is much more curved than in the left. (Pl. II. figs. 7 & 8.)

The otoliths of the 93-cm. eel are very curious, and the form of the antirostrum, rostrum, dorsal, ventral, and posterior rims all differ. The dorsal rim of the left otolith have few indentations, but that of the right one is serrated. In the left otolith the sulcus opens out narrowly on to the dorsal side of the rostrum and reaches the posterior rim, but in the right otolith the opening covers the greater part of the frontal rim, and the sulcus does not reach the posterior rim. (Pl. II. figs. 11 & 12.)

A very curious case is that of the otoliths of the 85-cm. eel. The antirostrum forms a point in the left otolith and is flattened in the right. In both otoliths the antirostrum has a small notch, in the left otolith below the point and in the right the notch divides the flattened antirostrum. In the left otolith the rostrum is obtuse and in the right pointed. The form of the sulcus differs also. (Pl. IV. figs. 21 & 22.)

EXHIBITIONS AND NOTICES.

October 21st, 1930.

Prof. E. W. MacBride, M.A., F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1930:—

May.

The registered additions to the Society's Menagerie during the month of May were 648 in number. Of these 146 were acquired by presentation, 392 were purchased, 37 were deposited, 17 were received in exchange, and 56 were born in the Menagerie.

The following may be specially mentioned:—

A Pigmy Hippopotamus, ♀ (*Chœropsis liberiensis*), born in the Gardens on May 10th.

8 Spotted Deer (*Axis axis*) and 14 Blackbuck (*Antilope cervicapra*), from India, and 5 Persian Gazelles (*Gazella subgutturosa*), from Persia, presented by Alfred Ezra, Esq., O.B.E., F.Z.S., on May 12th.

1 Californian Sea-Lion (*Zalophus californianus*), born in the Gardens on May 23rd.

1 Southern Elephant-Seal (*Mirounga leonina*), from the Falkland Islands, presented by G. A. S. Bennett, Esq., on May 27th.

1 Banksian Cockatoo (*Calyptorhynchus banksii*), from Australia; 2 Spix's Macaws (*Cyanopsitta spixii*), from Bahia, and 1 Rose-crested Cockatoo (*Kakatoë moluccensis*), from Ceram, presented by The Marquess of Cholmondeley, F.Z.S., on May 30th.

June.

The registered additions to the Society's Menagerie during the month of June were 658 in number. Of these 294 were acquired by presentation, 282 were purchased, 27 were deposited, 25 were received in exchange, and 30 were born in the Menagerie.

The following may be specially mentioned:—

1 Topi Antelope (*Damaliscus korrigum topi*), from Uganda, presented by Sir William F. Gowers, K.C.M.G., on June 7th.

2 Tigers (*Felis tigris*), from India, presented by Mr. & Mrs. A. G. Glenister on June 27th.

An important collection of Mammals including a Hardwick's Civet-Cat (*Hemigalus hardwickii*), Birds, and Reptiles, from the Federated Malay States, presented by A. St. Alban Smith, Esq., F.Z.S., on June 27th.

2 Wolverines (*Gulo gulo*), from Finland, purchased on June 30th.

July.

The registered additions to the Society's Menagerie during the month of July were 260 in number. Of these 57 were acquired by presentation, 52 were purchased, 31 were deposited, 13 were received in exchange, and 107 were born in the Menagerie.

The following may be specially mentioned :—

1 Cheetah (*Acinonyx jubatus*), from Kenya, presented by G. S. Cooke, Esq., on July 5th.

1 Female Chimpanzee (*Pan satyrus*), from the Cameroons, presented by A. A. Haserick, F.Z.S., on July 5th.

1 Grevy's Zebra (*Equus grevyi*), born in the Menagerie on July 15th.

August.

The registered additions to the Society's Menagerie during the month of August were 361 in number. Of these 261 were acquired by presentation, 37 were purchased, 28 were deposited, 15 were received in exchange, and 20 were born in the Menagerie.

The following may be specially mentioned :—

A large and valuable collection of Mammals, Birds, and Reptiles, many of which are new to the Collection, presented by A. St. Alban Smith, Esq., F.Z.S.

2 Duyvenbode's Lories (*Chalcopsitta duyvenbodei*), from New Guinea, purchased on August 2nd.

1 Black-crested Eagle (*Lophaëtus occipitalis*), from the Ituri forest, presented by R. Akroyd, Esq., on August 8th.

2 Saddle-billed Storks (*Ephippiorhynchus senegalensis*), from Sudan, purchased August 20th.

September.

The registered additions to the Society's Menagerie during the month of September were 261 in number. Of these 83 were acquired by presentation, 88 were purchased, 48 were deposited, 2 were received in exchange, and 50 were born in the Menagerie.

The following may be specially mentioned :—

An Anoa (*Anoa depressicornis*), born in the Menagerie on September 10th.

A Mongolian Wild Horse (*Equus caballus przewalskii*), born in the Menagerie on September 14th.

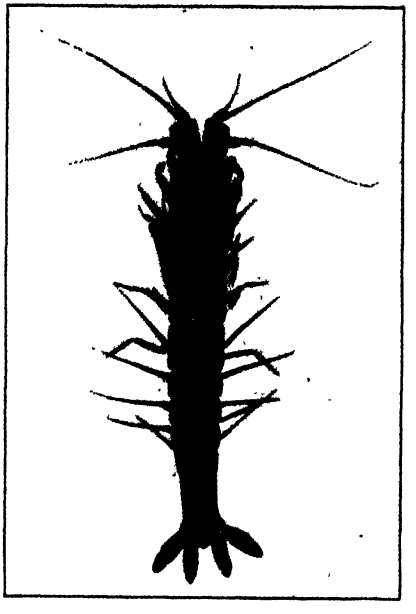
A Babirussa (*Babirussa babirussa*), from Celebes, purchased on September 20th.

3 Lion Cubs (*Felis leo*), born in the Menagerie on September 23rd.

A White cheeked Gibbon (*Hylobates leucogenys*), from Hainan, purchased on September 30th.

A Wilson's Bird-of-Paradise (*Schlegelia wilsoni*), a Magnificent Bird-of-Paradise (*Diphyllodes magnificus magnificus*), and a Papuan Frogmouth (*Podargus papuensis*), all from New Guinea, purchased on September 20th.

Dr. W. T. Calman, F.R.S., F.Z.S., on behalf of Miss S. M. Manton, M.A., Ph.D., exhibited a photograph of a living *Anaspides tasmaniæ* starting to swim, showing the metachronial rhythm of the pleopods. When swimming the pleopods beat in series with one another, but at different phases, the rhythm passing from behind forwards. In the accompanying photograph the first pair of pleopods are about to commence the backward stroke, while the second and third pairs are at



Photograph of a living *Anaspides tasmaniæ* starting to swim, showing the metachronial rhythm of the pleopods. (Enlarged about × 1·4.)

different phases, those behind having completed more of the backward stroke than those in front. The fourth and fifth pairs of pleopods show progressively advancing phases of the beat, the fourth being in the middle of the forward stroke while the fifth pair is almost ready to start the backward stroke again.

The normal position of rest of the pleopods is shown in plate ii. page 791 (Manton, S. M., "Notes on the Habits and Feeding Mechanisms of *Anaspides* and *Paranaspides*," P. Z. S. 1930, p. 791).

Prof. T. Thomson Flynn, D.Sc., exhibited, and made remarks upon, a unique collection of embryonic developmental material from the Echidna (*Tachyglossus*).

November 4th, 1930.

Prof. E. W. MacBride, M.A., F.R.S., Vice-President, in the Chair.

Mr. W. B. Cotton, I.C.S., F.Z.S., exhibited, and made remarks upon, the ears and molars of an African Elephant.

The SECRETARY exhibited, and made remarks upon, a series of photographs of African Elephants taken by Mr. M. A. Wetherall in the Belgian Congo.

Mr. J. R. NORMAN, F.Z.S, exhibited, and made remarks upon, photographs of a living Shark with a Remora attached.

Mr. E. G. BOULENGER, F.Z.S., exhibited, and made remarks upon, (1) a red variety of the Common Lobster, and (2) some eggs laid in the Society's Aquarium by a Sea-Snake (*Laticauda colubrina*).

November 18th, 1930.

Sir ARTHUR SMITH WOODWARD, LL.D., F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of October, 1930:—

The registered additions to the Society's Menagerie during the month of October were 144 in number. Of these 91 were acquired by presentation, 4 were purchased, 20 were deposited, 10 were received in exchange, and 19 were born in the Menagerie.

The following may be specially mentioned:—

A Wild Boar, ♀ (*Sus scrofa*), from Iraq, presented by J. W. Allcard, Esq., on October 13th.

A Cape Buffalo, ♂ (*Syncerus caffer*), born in the Gardens on October 13th.

A collection of Rodents, from Canada, including American and Prairie Marmots, Canadian Porcupines, and Fox-Squirrels, presented by the Toronto Parks Committee on October 27th.

2 White-fronted Sheld-Ducks (*Casarca cana*), from South Africa, presented by H.M. Office of Works, on October 3rd.

9 Jobi Island Ground-Doves (*Gallicolumba jobiensis*), new to the Collection, from Jobi Island, received in exchange on October 16th.

The SECRETARY exhibited, and made remarks upon, a photograph of a House-Sparrow (*Passer domesticus* Linn.) with an abnormal growth of beak.

Prof. R. T. LEIPER, D.Sc., M.D., F.R.S., F.Z.S., exhibited a series of lantern-slides illustrating Helminth infection in the brain of Man.

Dr. F. A. BATHER, F.R.S., F.Z.S., made remarks upon, and gave a general *résumé* of the Resolutions on Zoological Nomenclature passed at the Zoological Congress at Padua, 1930.

[Proceedings, 1930, Part III. (pp. 549–848), was published on October 22nd, 1930.]

INDEX OF ILLUSTRATIONS.

Abrana cotti, Fig. 1, p. 899.
Anaspides tasmaniæ, Pls. II.–IV., p. 791; Fig. 1, p. 1079.
Archelon ischyros, Pl. III., p. 1057.
Arrhenurus iniquus, Figs. 16–18, pp. 925–927.
—— *procerus*, Figs. 14, 15, p. 924.

Caretta caretta, Pl. II., p. 1057.
Cochlicella acuta, Pl. I., p. 1027.
Cocytinus gyrinoides, Pl. VI., p. 849; Fig. 21, p. 883.
Colosteus scutellatus. Pl. II., p. 849; Figs. 6, 7, p. 859.
Cryptochætum iceryæ, Pls. I.–V., p. 929; Figs. 1–23, pp. 931, 932, 940-942, 946, 949-952, 954, 959, 964, 965.

Dermochelys coriacea, Pl. I., p. 1057.
Development of the Heart of the Rabbit, Pls. I.–XI., p. 755.

Elephantolæmus indicus, Figs 1-3, pp. 678, 680 681.
Emyda granosa ceylonsis, Pl. II., p. 1057.
Ephestiasula intermedia, Pl. I., Fig. 4, p. 689.
Erpetosaurus lævis, Pl. I., p. 849; Figs. 4, 5, p. 857.
—— *radiatus*, Pl. I., p. 849; Figs. 1–3, pp. 853–855.

Hestiasula nigrofemorata, Pl. I., Figs. 2, 3, p. 689.
Hydrarachna eldoretica, Fig. 6, pp. 9, 18.
—— *spinosa* var. *subtilis*, Figs. 1–5, pp. 915–917.
Hyperolius argus, Pl. I., p. 897.
—— *mossambicus*, Pl. I., p. 897.

Lepidosiren paradoxa, Pl. I., p. 783.
Limnesia rugosa, Figs. 7–9, pp. 919, 920.

Macaca radiata, Uterus of, Pt. II., p. 691.
Mantis inornata, Pl. I., Fig. 1, p. 689.
Mytaras macrognathus, Pl. III., p. 849; Fig. 14, p. 868.

Ophiderpeton amphiuminus, Pl. V., p. 849; Fig. 17, p. 875.
Oryctolagus cuniculas, Development of Heart, Pls. I.–XI., p. 755.
Otoliths of some large Eels from the Lake of Tunis, Pls. I.–IV., p. 1071.

Palæospondylus, Fig. 5, p. 787.
Papio hamadryas, Ovary of, Pl. I., p. 691.
Paranaspides lacustris, Pl. I., p. 791.
Paraphædon tumidulus, Pls. I.–IV., p. 627; Figs. 1–17, pp. 634, 636, 637, 642, 643, 645, 647, 651, 653, 654, 656, 658, 660-662, 667–670.
Pelion lyelli, Pl. IV., p. 849; Figs. 15, 16, pp. 870. 871.
Piona crassipes, Figs. 10–13, pp. 922, 923.
Platyrhinops mordax, Pl. III., p. 849; Figs. 11–13, pp. 866, 867.
Pleuroptyx clavatus, Pl. VI., p. 849.
Protopterus, Fig. 3, p. 784.

Sauropleura marshii, Pl. VI., p. 849; Fig. 18, p. 878.
—— *pectinata*, Figs. 18–20, pp. 878–880.
Sciara nitidicollis, Figs. 1–14, pp. 1011–1024.
Sciurus carolinensis, Pl. I., p. 809.
Stegops divaricata, Pl. II., p. 849; Figs. 8–10, pp. 861–864.
Stenocypris malcomsoni, Pls. I., II., p. 973.

Triton vulgaris, Pl. I., p. 907.

INDEX.

1930.—Pages 549–1080.

[New names in clarendon type. Systematic references in italics. (z. s. l.) indicates additions to the Society's Menagerie.]

Abrana, gen. n., 898.
—— **cotti**, sp. n.., 898.
Abrornis affinis, 568.
—— *albosuperciliaris*, 568.
—— *castaneoceps*, 568.
—— *flaviventris*, 568.
—— *poligenys*, 568.
—— *schisticeps*, 568.
—— —— *schisticeps*, 568.
—— *superciliaris*, 568.
—— —— *salwinensis*, 568.
—— —— *superciliaris*, 568.
—— *xanthoschistos*, 568.
Acanthopneuste lugubris, 568.
—— *magnirostris*, 568.
—— *nitidus*, 568.
—— —— *nitidus*, 568.
—— *occipitalis*, 568.
—— *reguloides reguloides*, 568.
—— *trochiloides*, 568.
—— —— *trochiloides*, 568.
Acanthylis nudipes, 596.
Accentor altaicus, 574.
—— *himalayanus*, 574.
—— *immaculatus*, 574.
—— *nepalensis*, 574.
—— *nipalensis*, 574.
—— *rubeculoides*, 574.
—— *strophiatus*, 574.
Accipiter nisus, 604.
—— —— *melanochistus*, 604.
—— *virgatus*, 604.
—— —— *affinis*, 604.
—— —— *besra*, 604.
Aceros nepalensis, 598.
—— *nipalensis*, 598.
Acinonyx jubatus (z. s. l.), 1078.
Acridotheres fuscus, 554.
—— *ginginianus*, 554.
—— *tristis*, 554.
Acrocephalus arundinaceus orientalis, 566.
—— *brunnescens*, 566.
—— *dumetorum*, 566.
—— *orientalis*, 566.
—— *stentoreus*, 566.
—— —— *brunnescens*, 566.
Actinodura egertoni, 580.
—— —— *egertoni*, 580.
—— *nipalensis*, 580.
Actitis glareola, 612.
—— *hypoleucos*, 612.
—— *ochropus*, 612.
Adelura cæruleocephala, 572.
Ægialitis alexandrina, 614.
—— *cantianus*, 614.
—— *dubia*, 614.
—— *mongolica*, 614.
—— *philippensis*, 614.
—— *pyrrothorax*, 614.
Ægithaliscus concinnus iredalei, 564.
—— *erythrocephalus*, 564.
—— *ioschistos*, 564.
—— *niveogularis*, 564.
Ægithina tiphia, 582.
—— —— *tiphia*, 582.
Ægypius monachus, 582.
Æsalon chicquera, 606.
Æthalochora ashmoliana, 689.
Æthiopsa fuscus fuscus, 554.
Æthopyga gouldiæ, 560.
—— *ignicauda*, 560.

Æthopyga miles, 660.
—— *nepalensis*, 560.
—— *nipalensis nipalensis*, 560.
—— *saturata*, 560.
—— —— *saturata*, 560.
—— *seheriæ*, 560.
—— *siparaja seheriæ*, 560.
Aethorynchus lafresnayi, 582.
Agrodroma campestris, 560.
—— *sordida*, 560.
Agropsar sturninus, 552.
Alauda arvensis, 558.
—— —— *dulcivox*, 558.
—— *gulgula*, 558.
—— —— *gulgula*, 558.
—— *triborhyncha*, 558.
Alcedo atthis bengalensis, 598.
—— *bengalensis*, 598.
—— *ispida*, 598.
Alcippe nepalensis nepalensis, 580.
—— *nipalensis*, 580.
—— *phœocephala*, 580.
—— *poiocephala*, 580.
—— *poioicephala*, 580.
Alcurus striatus, 584.
Alectoris græca chukar, 620.
Allotrius œnobarbus, 582.
Alseonax ferrugineus, 586.
—— *latirostris*, 588.
—— —— *pœensis*, 588.
—— *ruficaudus*, 588.
Alsocomus elphinstonii, 620.
—— *hodgsonii*, 620.
—— *pulchricollis*, 620.
—— *puniceus*, 620.
Alytes obstetricans, 845.
Amandava amandava, 566.
Amaurornis akool, 618.
—— —— *akool*, 618.
—— *fuscus*, 618.
—— —— *fuscus*, 618.
—— *phœnicurus*, 618.
—— —— *phœnicurus*, 618.
Ampeliceps coronatus, 552.
Anas acuta, 610.
—— —— *acuta*, 610.
—— *angustirostris*, 608.
—— *boscas*, 608.
—— *crecca*, 608.
—— *penelope*, 608.
—— *platyrhyncha*, 608.
—— *platyrhynchos platyrhynchos*, 608.
—— *pœcilorhyncha* 608.
Anas pœcilorhyncha pœcilorhyncha, 608.
—— *querquedula*, 608.
Anaspides tasmaniæ, 791, 1078.
Anastomus oscitans, 610.
Anhinga melanogaster, 608.
Anoa depressicornis (Z. S. L.), 1078.
Anorthura nepalensis, 574.
Anser anser, 608.
—— *cinereus*, 608.
—— *ferus*, 608.
—— *indicus*, 608.
Anthipes monileger, 588.
—— —— *monileger*, 588.
—— —— *submonileger*, 588.
—— *submonileger*, 588.
Anthracoceros albirostris, 598.
—— *malabaricus malabaricus*, 598.
Anthropoides virgo, 612.
Anthus campestris, 560.
—— —— *campestris*, 560.
—— *cervinus*, 560.
—— *hodgsoni hodgsoni*, 560.
—— *maculatus*, 560.
—— *nilghiriensis*, 560.
—— *richardi*, 560.
—— —— *godlewskii*, 560.
—— —— *richardi*, 560.
—— —— *rufulus*, 560.
—— —— *striolatus*, 560.
—— *rosaceus*, 560.
—— *roseatus*, 560.
—— *rufulus*, 560.
—— *similis*, 560.
—— *sordidus jerdoni*, 560.
—— *striolatus*, 560.
—— *trivialis*, 560.
—— —— *trivialis*, 560.
Antigone antigone antigone, 612.
Antilope cervicapra (Z. S. L.), 846, 1077.
Aquila bifasciata, 604.
—— *chrysaëtos*, 604.
—— —— *daphanea*, 604.
—— *clanga*, 604.
—— *fulvescens*, 604.
—— *heliaca*, 604.
—— —— *heliaca*, 604.
—— *imperialis*, 604.
—— *maculata*, 604.
—— *nœvia*, 604.
—— *nipalensis nipalensis*, 604.
—— *rapax vindhiana*, 604.
—— *vindhiana*, 604.
Arachnechthra asiatica, 560.

Arachnechthra flammaxillaris, 562.
—— *hasselti*, 560.
—— *lotenia*, 560.
—— *minima*, 560.
—— *zeylonica*, 560.
Arachnothera magna, 562.
—— —— *magna*, 562.
Arborophila brunneipectus, 622.
—— *brunneopectus brunneopectus*, 622.
—— *rufigularis*, 622.
—— *rufogularis*, 622.
—— —— *rufogularis*, 622.
—— *torqueola*, 622.
—— —— *torqueola*, 622.
Arceuthornis viscivorus bonapartei, 574.
Archelon ischyros, 1058.
Ardea cinerea, 610.
—— —— *rectirostris*, 610.
—— *manillensis*, 610.
—— *purpurea*, 610.
—— —— *manillensis*, 610.
—— *sumatrana*, 610.
—— —— *sumatrana*, 610.
Ardeola grayii, 610.
—— *leucoptera*, 610.
Ardetta cinnamomea, 610.
—— *flavicollis*, 610.
—— *minuta*, 610.
—— *sinensis*, 610.
Argya caudata, 578.
—— —— *caudata*, 578.
—— *earlii*, 578.
—— *longirostris*, 578.
—— *malcolmi*, 578.
Arrhenurus iniquus, sp. n., 925.
—— procerus, sp. n., 923.
Artamus fuscus, 566.
Arthroleptis stenodactylus, 899.
Arundinax aedon, 566.
—— *olivaceus*, 566.
Asarcornis scutulatus, 608.
Ascornis scutulatus, 608.
Asio accipitrinus, 600.
—— *flammeus*, 600.
—— *otus*, 600.
—— —— *otus*, 600.
Astur badius, 604.
—— —— *dussumieri*, 604.
—— *gentilis schvedowi*, 604.
—— (*Lophospiza*) *trivirgatus*, 604.
—— *palumbarius*, 604.
—— *trivirgatus*, 604.
—— —— *ruficinctus*, 604.
Athene brama, 602.
—— —— *brama*, 602.
—— *cuculoides*, 602.
—— *malabarica*, 602.
—— *radiata*, 602.
Axis axis (Z. S. L.), 1077.
Aythya ferina, 610.
—— *nyroca*, 610.

Babirussa babirussa (Z. S. L.), 1078.
Batrachostomus hodgsoni, 600.
—— *javensis hodgsoni*, 600.
—— *monileger*, 600.
Baya leuphotes leuphotes, 606.
—— *lophotes*, 606.
Bhringa remifer, 554.
—— —— *tectirostris*, 554.
Blythipicus pyrrhotis pyrrhotis, 592.
Botaurus stellaris, 610.
—— —— *stellaris*, 610.
Brachypodius poiocephalus, 584.
Brachypternus aurantius, 592.
—— *benghalensis benghalensis*, 592.
Brachypteryx cruralis, 570.
—— *major major*, 570.
—— *nipalensis*, 570.
—— *rufiventris*, 570.
Branta rufina, 610.
Breviceps mossambicus, 905.
Briania hodgsoni hodgsoni, 586.
Bubo bengalensis, 602.
—— *bubo bengalensis*, 602.
—— *coromandus*, 602.
—— —— *coromandus*, 602.
—— *nipalensis*, 602.
Bubulcus coromandus, 610.
—— *ibis coromandus*, 610.
Bucia atherioni, 598.
Budytes citreola, 560.
—— *viridis*, 560.
Bufo regularis regularis, 905.
Buphus coromandus, 610.
Burhinus oedicnemus indicus, 612.
Butastur indicus, 604.
—— *teesa*, 604.
Buteo buteo vulpinus, 604.
—— *canescens*, 604.
—— *desertorum*, 604.
—— *ferox*, 604.
—— —— *ferox*, 604.
—— *rufinus rufinus*, 604.
—— *vulpinus*, 604.

Butorides javanicus, 610.
—— *striatus javanicus*, 610.

Caccabis chucar, 620.
—— *chukor*, 620.
Cacomantis merulinus, 594.
—— —— *passerinus*, 594.
—— —— *querulus*, 594.
—— *passerinus*, 594.
Calœnas nicobarica, 620.
Calandrella brachydactyla, 558.
—— —— *dukhunensis*, 558.
—— *dukhunensis*, 558.
Calidris alpina alpina, 614.
—— *minuta minuta*, 614.
—— *temminckii*, 614.
Callialcyon lilacina, 600.
Calliope calliope, 572.
—— *camtschatkensis*, 572.
—— *kamschatkensis*, 572.
—— *pectoralis*, 572.
—— —— *pectoralis*, 572.
Calobates sulphurea, 560.
Calornis chalybicus, 554.
Calyptomena viridis, 590.
—— —— *continentis*, 590.
Calyptorhynchus bankii (Z. S. L.), 1077.
Campophaga melanoptera, 586.
—— *melanoschista*, 586.
—— *sykesi*, 586.
Capella gallinago gallinago, 614.
—— *nemoricola*, 614.
—— *solitaria*, 614.
—— *stenura*, 614.
Caprimulgus albonotatus, 596.
—— *asiaticus*, 596.
—— *indicus*, 596.
—— —— *indicus*, 596.
—— *macrourus*, 596.
—— —— *albonotatus*, 596.
—— —— *nipalensis*, 596.
—— *macrurus*, 596.
—— —— *albonotatus*, 965.
—— —— *nipalensis*, 596.
—— *mahrattensis*, 598.
—— *monticola*, 598.
—— *monticolus*, 598.
—— —— *monticolus*, 598.
Carcineutes pulchellus, 600.
—— —— *pulchellus*, 600.
Cardueliscaniceps, 556.
Cardueliscaniceps caniceps, 556.
Carine brama brama, 602.
Carpodacus erythrinus, 556.
—— —— *roseatus*, 556.
Carpophaga ænea, 618.
—— *insignis*, 618.
—— *sylvatica*, 618.
Casarca cana (Z. S. L.), 1080.
—— *ferruginea*, 608.
—— *leucoptera*, 608.
—— —— *rutila*, 608.
Catreus wallichii, 624.
Centropus bengalensis, 596.
—— —— *bengalensis*, 596.
—— *rufipennis*, 596.
—— *sinensis*, 596.
—— —— *parroti*, 596.
—— —— *sinensis*, 596.
Cephalopyrus flammiceps, 564.
Cerchneis naumanni pekinensis, 606.
—— *tinnunculus interstinctus*, 606.
—— —— *objurgatus*, 606.
—— —— *tinnunculus*, 606.
Cercocebus, 700.
Cercomela fusca, 570.
Cercopithecus, 699.
Ceriornis melanocephala, 622.
—— *satyra*, 622.
Certhia discolor, 562.
—— —— *discolor*, 562.
—— *familiaris hodgsoni*, 562.
—— —— *nipalensis*, 562.
—— *himalayana*, 562.
—— *hodgsoni*, 562.
—— *nepalensis*, 562.
—— *nipalensis*, 562.
Ceryle guttata, 598.
—— *guttulata*, 598.
—— *lugubris*, 598.
—— *rudis*, 598.
—— —— *leucomelanura*, 598.
—— *varia*, 598.
Ceyx erithaca erithaca, 598.
—— *tridactyla*, 598.
—— *tridactylus tridactylus*, 598.
Chœmorrornis leucocephala, 572.
Chœtura nudipes, 596.
Chaimarrhornis leucocephala, 572.
Chalcites maculatus maculatus, 594.
—— *xanthorhynchus*, 594.
Chalcoparia phœnicotis, 560.
—— *singalensis singalensis*, 560.
Chalcophaps indica, 620.

Chalcophaps indica indica, 620.
—— *indicus*, 620.
Chalcopsitta duyvenbodei (Z. S. L.), 1078.
Chaptia ænea, 554.
—— —— *ænea*, 554.
Charadrius alexandrinus seebohmi, 614.
—— *dubius jerdoni*, 614.
—— *fulvus*, 614.
—— *longipes*, 614.
Chatarrhœa caudata, 578.
—— *earlei*, 578.
Chaulelasmus streperus, 608.
Chelidon lagopus, 588.
—— *nepalensis*, 588.
—— *nipalensis*, 588.
Chelidorhynx hypoxanthum, 588.
Chettusia gregaria, 614.
—— *inornata*, 614.
—— *leucura*, 614.
Chibia hottentotta, 554.
—— —— *hottentotta*, 554.
Chiromantis xerampelina, 899.
Chlamydotis undulata macqueenii, 612.
Chleuasicus ruficeps, 582.
Chlidonias leucopareia indica, 616.
Chloropsis aurifrons, 582.
—— —— *aurifrons*, 582.
—— —— *davidsoni*, 582.
—— *hardwickii*, 582.
—— —— *hardwickii*, 582.
—— *jerdoni*, 582.
—— *malabarica*, 582.
—— *viridis zosterops*, 582.
—— *zosterops*, 582.
Chœropsis liberiensis (Z. S. L.), 846, 1077.
Choriotis nigriceps, 612.
Chrysococcyx hodgsoni, 594.
—— *maculatus*, 594.
—— *xanthorhynchus*, 594.
Chrysocolaptes festivus, 594.
—— *goensis*, 594.
—— *guttacristatus guttacristatus*, 592.
—— —— *sultaneus*, 594.
—— *gutticristatus*, 592, 594.
—— *sultaneus*, 594.
Chrysomitris spinoides, 554.
Chrysonotus shorei, 592.
Chrysophlegma chlorolophus, 592.
—— *chorolophus*, 592.
—— *flavinucha*, 592.
—— —— *flavinucha*, 592.
Ciconia alba, 610.
—— *ciconia ciconia*, 610.
Ciconia leucocephala, 610.
—— *nigra*, 610.
Cinclus asiaticus, 574.
—— *pallasii tenuirostris*, 574.
Circaëtus gallicus, 604.
Circus æruginosus, 604.
—— —— *æruginosus*, 604.
—— *cineraceus*, 604.
—— *cyaneus*, 604.
—— —— *cyaneus*, 604.
—— *macrourus*, 604.
—— *melanoleucos*, 604.
—— *melanoleucus*, 604.
—— *pygargus*, 604.
—— *swainsoni*, 604.
Cirrepidesmus mongolus atrifrons, 614.
Cissa chinensis, 552.
—— —— *chinensis*, 552.
—— *sinensis*, 552.
Cisticola cursitans, 566.
—— *juncidis cursitans*, 566.
—— *schœnicola*, 566.
Cittocincla macrura, 572.
Clamator coromandus, 594.
—— *jacobinus jacobinus*, 594.
Cobboldia elephantis, 683.
—— *loxodontis*, 684.
Coccystes coromandus, 594.
—— *jacobinus*, 594.
—— *melanoleucos*, 594.
Cochlicella acuta, 1027.
Cochoa purpurea, 574.
—— *viridis*, 574.
Cocytinus gyrinoides, 882.
Collocalia brevirostris, 596.
—— *fuciphaga*, 596.
—— —— *brevirostris*, 596.
—— *nidifica*, 596.
—— *unicolor unicolor*, 596.
Colosteus scutellatus, 858.
Columba elphinstonii, 620.
—— *eversmanni*, 618.
—— *hodgsonii*, 618.
—— *intermedia*, 618.
—— *leuconota*, 618.
—— —— *leuconota*, 618.
—— *livia intermedia*, 618.
—— *œnas eversmanni*, 618.
—— *palumbus casiotis*, 620.
—— *pulchricollis*, 620.
—— *puniceus*, 618.
Conostomus æmodium, 582.
Copsychus saularis, 572.

Copsychus saularis saularis, 572.
Coracias affinis, 598.
—— *benghalensis affinis*, 598.
—— —— *benghalensis*, 598.
—— *indica*, 598.
Coracina macei macei, 586.
—— —— *nipalensis*, 586.
Corvus corax, 552.
—— —— *tibetanus*, 552.
—— *coronoides culminatus*, 552.
—— —— *intermedius*, 552.
—— —— *levaillanti*, 552.
—— —— *levaillantii*, 552.
—— *culminatus*, 552.
—— *intermedius*, 552.
—— *macrorhynchus*, 552.
—— *splendens*, 552.
—— —— *splendens*, 552.
Corydalla richardi, 560.
—— *rufula*, 560.
—— *striolata*, 560.
Corydon sumatranus, 590.
—— —— *sumatranus*, 590.
Coryllis vernalis rubropygialis, 600.
—— —— *vernalis*, 600.
Corythocichla brevicauda, 578.
Cotile sinensis, 588.
Coturnix communis, 622.
—— *coromandelica*, 622.
—— *coturnix coturnix*, 622.
—— —— *japonica*, 622.
Cotyle rupestris, 588.
—— *sinensis*, 588.
Crateropus canorus, 578.
Criniger burmanicus, 584.
—— *flaveolus*, 582.
—— *ictericus*, 584.
—— *tephrogenys burmanicus*, 584.
—— —— *flaveolus*, 582.
Crocopus phœnicopterus, 618.
—— —— *phœnicopterus*, 618.
—— —— *viridifrons*, 618.
Crossoptilon crossoptilon crossoptilon, 624.
—— *tibetanus*, 624.
Crypsirhina cucullata, 552.
—— *varians*, 552.
Cryptochastum iceryæ, 929.
Cryptolopha affinis, 568.
—— *burkii*, 568.
—— *castaneiceps*, 568.
—— *cinereocapilla*, 568.
—— *jerdoni*, 568.
—— *poliogenys*, 568.
Cryptolopha xanthoschista, 568.
Cryptoplectron erythrorhynchum erythrorhynchum, 622.
Cuculus canorus, 594.
—— —— *telephonus*, 594.
—— *himalayanus*, 594.
—— *micropterus*, 594.
—— —— *micropterus*, 594.
—— *poliocephalus*, 594.
—— —— *poliocephalus*, 594.
—— *sonneratii*, 594.
Culicicapa ceylonensis, 588.
—— —— *ceylonensis*, 588.
Culicipeta burkii, 568.
Cuncuma leucogaster, 606.
Cursonia crispifrons, 578.
Cursorius coromandelicus, 616.
Cutia nipalensis, 582.
—— —— *nipalensis*, 582.
Cyanecula suecica, 572.
Cyaneula suecica, 572.
Cyanops asiatica, 590.
—— —— *asiatica*, 590.
—— *franklinii*, 580.
—— —— *franklinii*, 590.
—— —— *ramsayi*, 590.
—— *ramsayi*, 590.
Cyanopsitta spixii (Z. S. L.), 1077.
Cyanosylvia suecica suecica, 572.
—— *svecica svecica*, 572.
Cygnus cygnus, 608.
—— *musicus*, 608.
Cymbirhynchus macrorhynchus macrorhynchus, 590.
Cymborhynchus macrorhynchus, 590.
Cynopithecus, 708.
Cyornis banyumas, 586.
—— *hyperythra hyperythra*, 586.
—— *hyperythrus*, 586.
—— *leucomelanurus*, 586.
—— *magnirostris*, 586.
—— *melanoleuca melanoleuca*, 586.
—— *melanoleucus*, 586.
—— —— *westermanni*, 586.
—— *rubeculoides*, 586.
—— —— *rubeculoides*, 586.
—— *ruficauda*, 588.
—— *sapphira*, 586.
—— *superciliaris*, 586.
—— *tickellice tickellice*, 586.
—— *tickellii*, 586.
—— *tricolor tricolor*, 586.
Cypselus affinis, 596.

Cypselus batassiensis, 596.
—— *leuconyx*, 596.
—— *melba*, 596.
—— *pacificus*, 596.
Cypsiurus balasiensis balasiensis, 596.

Dafila acuta, 610.
—— —— *acuta*, 610.
Damaliscus korrigum topi (Z. S. L.), 1077.
Delichon nepalensis, 588.
—— *nipalensis*, 588.
—— *urbica whiteleyi*, 588.
Demiegretta sacra sacra, 610.
Demigretta sacra sacra, 610.
Dendrobates tinctorius, 845.
Dendrochelidon coronatus, 596.
Dendrocitta frontalis, 552.
—— *himalayensis*, 552.
—— *leucogastra*, 552.
—— *rufa*, 552.
—— —— *rufa*, 552.
—— —— *vagabunda*, 552.
—— *sinensis*, 552.
—— —— *assimilis*, 552.
—— —— *himalayensis*, 552.
Dendrocopus atratus, 592.
—— *auriceps*, 592.
—— *cathpharius*, 592.
—— *darjilensis*, 592.
—— *himalayensis*, 592.
Dendrocygna arcuata arcuata, 608.
—— *awsuree*, 608.
—— *javanica*, 608.
—— *major*, 608.
Dendronanthus indicus, 560.
Dendrophassa bicincta bicincta, 618.
—— *pompadora affinis*, 618.
—— —— *phayrei*, 618.
Dendrophila frontalis, 564.
Dendrotreton hodgsoni, 620.
—— *hodgsonii*, 620.
Dermochelys coriacea, 1057.
Diardigallus diardi, 624.
Dicæum chrysorrhœum, 562.
—— —— *chrysochlore*, 562.
—— —— *intensum*, 562.
—— *coccineum*, 562.
—— *concolor*, 562.
—— *cruentatum*, 562.
—— —— *cruentatum*, 562.
—— —— *ignitum*, 562.
—— *erythrorhynchos erythrorhynchos*, 562.
Dicæum erythrorhynchum erythrorhynchum, 562.
—— *erythrorhynchus*, 562.
—— *ignipectum ignipectum*, 562.
—— *ignipectus*, 562.
—— *minimum*, 562.
—— *minullum concolor*, 562.
—— *trigonostigma*, 562.
—— —— *rubropygium*, 562.
Dichoceros bicornis, 598.
—— —— *bicornis*, 598.
Dicrurus annectens, 554.
—— *ater*, 554.
—— *balicassius*, 554.
—— *cærulescens*, 554.
—— *leucophœus longicaudatus*, 554.
—— —— *nigrescens*, 554.
—— *longicaudatus*, 554.
—— *macrocercus*, 554.
—— —— *albirictus*, 554.
—— —— *macrocercus*, 554.
—— *nigrescens*, 554.
Dinopicus shorii, 592.
Dionopium shorii, 592.
Diphyllodes magnificus magnificus (Z. S. L.), 1078.
Dissemurus paradiseus, 554.
—— —— *grandis*, 554.
—— —— *malabaricus*, 554.
—— —— *paradiseus*, 554.
Dissoura episcopa episcopa, 612.
—— *episcopus*, 610.
Drymochares cruralis, 570.
—— *nipalensis*, 570.
Drymoica jerdoni, 570.
Drymoipus inornatus, 570.
—— *sylvaticus*, 568.
Dryobates atratus, 592.
—— *auriceps*, 592.
—— *cathparius cathparius*, 592.
—— *cathpharius*, 592.
—— *darjellensis*, 592.
—— *himalayensis himalayensis*, 592.
—— *macei atratus*, 592.
—— —— *westermani*, 592.
Dryonastes chinensis, 576.
—— —— *leucogenys*, 576.
—— *cærulatus*, 576.
—— —— *cærulatus*, 576.
—— *ruficollis*, 576.
Ducula badia insignis, 618.
—— *insignis*, 618.
Dumetia hyperythra, 578.

Dupetor flavicollis, 610.
—— —— *flavicollis*, 610.

Edolius malabaricus, 554.
—— *paradiseus*, 554.
Egretta alba, 610.
—— *garzetta garzetta*, 610.
—— *intermedia intermedia*, 610.
Elanus cæruleus, 606.
—— —— *vociferus*, 606.
—— *milanopterus*, 606.
Elephantolcamus, gen. n., 679.
—— **indicus**, sp. n., 680.
Emberiza aureola, 558.
—— *fucata*, 558.
—— —— *arcuata*, 558.
—— *icterica*, 558.
—— *luteola*, 558.
—— *nemoricola*, 558.
—— —— *nemoricola*, 558.
—— *pusilla*, 558.
—— *stewarti*, 558.
Emyda granosa ceylonensis, 1057.
Enicurus immaculatus, 570.
—— *maculatus*, 570.
—— —— *guttatus*, 560.
—— —— *maculatus*, 570.
—— *nigrifrons*, 570.
—— *schistaceus*, 570.
—— *scouleri*, 570.
Entomothera coromanda coromanda, 600.
Eomantis guttatipennis, 689.
Ephestiasula intermedia, sp. n., 690.
Ephialtes lempigi, 602.
—— *pennatus*, 602.
Ephippiorhynchus senegalensis (Z. S. L.), 1078.
Equus cabbalus przewalskii (Z. S. L.), 1078.
—— *grevyi* (Z. S. L.), 1078.
Eremopterix grisea, 558.
Erolia alpina alpina, 614.
—— *temminckii*, 614.
Erpetosaurus lævis, 856.
—— *raaiatus*, 852.
Erpornis xantholeuca, 580.
—— —— *xantholeuca*, 580.
Erythrocebus, 699.
Erythropus amurensis, 606.
—— *cenchris*, 606.
—— *vespertinus*, 606.
Erythrosterna leucura, 586.
—— *maculata*, 586.

Esacus recurvirostris, 612.
Estrelda amandava, 556.
—— *formosa*, 556.
Eudynamis honorata, 594.
—— *scolopaceus scolopaceus*, 594.
Eudynamys orientalis, 594.
Eulabes intermedia, 554.
—— *javana intermedia*, 554.
—— *religiosa*, 554.
Eumyias albicaudata, 586.
—— *melanops*, 586.
Eupodotis edwardsii, 612.
Eurylæmus javanicus, 590.
Eurylaimus javanicus harterti, 590.
—— —— *javanicus*, 590.
Eurystomus orientalis, 598.
—— —— *orientalis*, 598.
Euspiza aureola, 558.
—— *luteola*, 558.
Excalfactoria chinensis, 622.
—— —— *chinensis*, 622.
Exocœtus fernandezianus, 847.

Falcinellus igneus, 612.
Falco babylonicus, 606.
—— *barbarus*, 606.
—— (*Cerchneis*) *tinnunculus interstinctus*, 606.
—— (——) —— *objurgatus*, 606.
—— (——) —— *tinnunculus*, 606.
—— *cherug*, 606.
—— —— *cherug*, 606.
—— *chicquera chicquera*, 606.
—— (*Erythropus*) *amurensis*, 606.
—— *jugger*, 606.
—— *naumanni pekinensis*, 606.
—— *peregrinator*, 606.
—— *peregrinus*, 606.
—— —— *calidus*, 606.
—— —— *pelegrinoides*, 606.
—— —— *peregrinator*, 606.
—— *saker*, 606.
—— *severus*, 606.
—— —— *rufipedoides*, 606.
—— *subbuteo*, 606.
—— —— *subbuteo*, 606.
Felis leo (Z. S. L.), 845, 1078.
—— *tigris* (Z. S. L.), 1077.
Francolinus chinensis, 622.
—— *francolinus asiæ*, 620.
—— —— *melanotus*, 622.
—— *gularis*, 622.

Francolinus pintadeanus phayrei, 622.
—— *pondicerianus*, 622.
—— —— *interpositus*, 622.
—— —— *pondicerianus*, 622.
—— *vulgaris*, 622.
Franklinia buchanani, 566.
—— *cinereicapilla*, 566.
—— *cinereocapilla*, 566.
—— *gracilis*, 566.
—— *hodgsoni*, 566.
Eregilus himalayanus, 552.
Fringillauda nemoricola, 558.
—— —— *nemoricola*, 558.
Fulica atra, 618.
—— —— *atra*, 618.
Fuligula cristata, 610.
Fulvetta vinipecta vinipecta, 580.

Galachrysia lactea, 616.
Galerida cristata, 558.
—— —— *chendoola*, 558.
Gallicolumba jobiensis (Z. S. L.), 1080.
Gallicrex cinerea, 618.
—— *cristatus*, 618.
Gallinago cœlestis, 614.
—— *gallinula*, 614.
—— *nemoricola*, 614.
—— *scolopacinus*, 614.
—— *solitaria*, 614.
—— *stenura*, 614.
Gallinula chloropus, 618.
—— —— *indicus*, 618.
—— *phœnicura*, 618.
Galloperdix lunulata, 622.
—— *lunulosus*, 622.
—— *spadicea*, 622.
—— —— *spadicea*, 622.
—— *spadiceus*, 622.
Gallophasis albocristatus, 622.
—— *melanotus*, 622.
Gallus bankiva murghi, 624.
—— —— *robinsoni*, 624.
—— *ferrugineus*, 624.
—— *gallus murghi*, 624.
—— —— *robinsoni*, 624.
—— *sonnerati*, 624.
Gampsorhynchus rufulus, 578.
—— —— *rufulus*, 578.
—— —— *torquatus*, 578.
—— *torquatus*, 578.
Garrulax albogularis, 576.
—— *belangeri*, 576.
Garrulax cœrulatus, 576.
—— *leucolophus*, 576.
—— —— *belangeri*, 576.
—— —— *leucolophus*, 576.
—— *moniliger*, 576.
—— —— *moniliger*, 576.
—— *ocellatus*, 576.
—— *pectoralis*, 576.
—— —— *pectoralis*, 576.
—— *ruficollis*, 576.
—— *strepitans*, 576.
Garrulus bispecularis, 552.
—— —— *bispecularis*, 552.
—— —— *interstinctus*, 552.
—— *lanceolatus*, 552.
Gazella subguttatus (Z. S. L.), 1077.
Gecinulus grantia, 592.
—— —— *grantia*, 592.
Gecinus chlorogaster, 592.
—— *chlorolophus*, 590, 592.
—— *occipitalis*, 592.
—— *squamatus*, 592.
—— *striolatus*, 592.
—— *viridanus*, 592.
Gelochelidon anglicus, 616.
—— *nilotica nilotica*, 616.
Gennæus albicristatus, 624.
—— *hamiltoni*, 624.
—— *horsfieldi*, 624.
—— —— *cuvieri*, 624.
—— *leucomelanus*, 624.
—— *lineatus*, 624.
—— —— *lineatus*, 624.
—— *melanonotus*, 624.
—— *melanotus*, 624.
Geocichla citrina, 574.
—— —— *citrina*, 574.
—— —— *cyanotis*, 574.
—— *cyanonotus*, 574.
—— *cyanota*, 574.
—— *unicolor*, 572.
—— *wardi*, 574.
Geocmyda trijuga thermalis, 1057.
Geokichla citrina citrina, 574.
—— —— *cyanotis*, 574.
—— *wardi*, 574.
Geronticus papillosus, 574.
Glareola lactea, 616.
—— *maldivarum maldivarum*, 616.
—— *orientalis*, 616.
Glaucidium brodiei, 602.
—— —— *brodiei*, 602.
—— —— *tubiger*, 602.

Glaucidium cuculoides, 602.
—— —— *cuculoides*, 602.
—— *radiatum*, 602.
—— —— *malabaricum*, 602.
—— —— *radiatum*, 602.
Glottis nebularia, 612.
Gorilla, 697.
Gracula javana intermedia, 554.
—— *religiosa*, 554.
Graculus carbo, 608.
—— *eremita*, 552.
—— *javanicus*, 608.
Grammatoptila striata, 578.
—— —— *striata*, 578.
Grandala cœlicolor, 572.
Graucalus macei, 586.
—— —— *macei*, 586.
—— —— *nipalensis*, 586.
Grus antigone, 612.
—— *cinerea*, 612.
—— *communis*, 612.
—— *grus lilfordi*, 612.
Gulo gulo (Z. S. L.), 1077.
Gymnorhis flavicollis, 556.
Gymnoris xanthocollis xanthocollis, 556.
Gypaëtus barbatus, 604.
—— —— *hemachalanus*, 604.
Gyps bengalensis, 602.
—— *indicus*, 602.
—— —— *indicus*, 602.
Gypsophila crispifrons, 578.

Hæmatopus ostralegus, 614.
—— —— *ostralegus*, 614.
Hæmatospiza indica, 556.
—— *sipahi*, 556.
Halcyon amauropterus, 600.
—— *atricapillus*, 600.
—— *coromandelianus*, 600.
—— *fuscus*, 600.
—— *leucocephalus*, 600.
—— *pileata*, 600.
—— *smyrnensis*, 600.
—— —— *fusca*, 600.
Haliaëtus fulviventer, 606.
—— *leucogaster*, 606.
—— *leucoryphus*, 606.
Haliastur indus, 606.
—— —— *indus*, 606.
Harpactes erythrocephalus, 596.
—— *fasciatus*, 596.
—— *hodgsoni*, 596.
Harpactes orescius, 596.
Heliopais personata, 618.
Hemerophila abruptaria var. *unicolor*, 847.
Hemicercus canente, 594.
—— —— *canente*, 594.
Hemichelidon cinereiceps, 586.
—— *ferruginea*, 586.
—— *fuliginosus*, 586.
—— *sibirica*, 586.
—— —— *sibirica*, 586.
Hemigalus hardwickii (Z. S. L.), 1077.
Hemilophus pulverulentis, 594.
Hemiprocne coronata, 596.
Hemipus picatus, 566.
—— —— *picatus*, 566.
Hemisus marmoratum, 905.
Hemixos flavala, 584.
—— *mcclellandi*, 584.
Hemixus flavala, 584.
—— —— *davisoni*, 584.
—— —— *flavala*, 584.
—— *mcclellandi*, 584.
—— —— *mcclellandi*, 584.
—— —— *tickelli*, 584.
—— *tickelli*, 584.
Henicurus guttatus, 570.
—— *immaculatus*, 570.
—— *maculatus*, 570.
—— *schistaceus*, 570.
Herodias alba, 610.
—— *egrettoides*, 610.
Herodius garzetta, 610.
—— *intermedia*, 610.
Herpornis xantholeuca, 580.
Hesperiphona affinis, 556.
Hestiasula brunneriana, 690.
—— nigrofemorata, sp. n., 690.
Heteroxenicus cruralis, 570.
—— *nipalensis nipalensis*, 570.
Heterura sylvana, 560.
Hieraëtus fasciatus, 604.
—— —— *fasciatus*, 604.
Hierax eutolmos, 604.
Hierococcyx fugax nisicolor, 594.
—— *nisicolor*, 594.
—— *sparveroides*, 594.
—— *varius*, 594.
Hilarocichla rufiventer, 582.
Himantopus candidus, 614.
Hirundapus caudacutus nudipes, 596.
Hirundo daurica, 588.
—— —— *erythropygia*, 588.
—— —— *nepalensis*, 588.

Hirundo daurica nipalensis, 588.
—— —— *striolata*, 588.
—— *domicola*, 588.
—— *erythropygia*, 588.
—— *filifera*, 588.
—— *javanica*, 588.
—— —— *domicola*, 588.
—— *nepalensis*, 588.
—— *rustica*, 588.
—— —— *rustica*, 588.
—— *smithii*, 588.
—— —— *filifera*, 588.
Hodgsonius phœnicuroides, 570.
—— —— *phœnicuroides*, 570.
Homraius bicornis, 598.
Hoplopterus ventralis, 614.
Horeites brunneifrons, 568.
—— *brunnifrons*, 568.
Horornis fortipes, 568.
—— —— *fortipes*, 568.
—— *fuliginiventer*, 566.
—— *pallida pallida*, 568.
—— *pallidus*, 568.
—— —— *pallidus*, 568.
Houbara macqueenii, 612.
Houbaropsis bengalensis, 612.
—— *indica*, 612.
Huhua nepalensis, 602.
—— *nipalensis*, 602.
Hydrarachna eldoretica, 918.
—— **spinosa, var. subtilis, var. n.**, 915.
Hydrobata asiatica, 574.
Hydrochelidon hybrida, 616.
—— *indica*, 616.
Hydrocichla frontalis, 570.
Hydrocissa albirostris, 598.
Hydrophasianus chirurgus, 616.
Hydroprogne caspia caspia, 616.
Hylambates maculatus, 900.
Hylobates leucogenys (Z. S. L.), 1078.
Hypacanthis spinoides, 556.
Hyperolius argus, 902.
—— *bayoni*, 902.
—— *concolor*, 902.
—— *marmoratus*, 902.
—— *microps*, 905.
—— **mossambicus, sp. n.**, 904.
Hypopicus hyperythrus, 592.
—— —— *hyperythrus*, 592.
Hypothymis azurea, 588.
—— —— *styani*, 588.
Hypotriorchis chiquera, 606.
Hypsipetes ganeesa, 584.
Hypsipetes mclellandi, 584.
—— *neilgherriensis*, 584.
—— *psaroides*, 584.

Ianthia cyanura, 572.
—— —— *rufilata*, 572.
—— *hyperythra*, 572.
—— *indica*, 572.
—— —— *indica*, 572.
—— *rufilata*, 572.
—— *superciliaris*, 572.
Ianthocincla ocellata, 576.
—— *rufogularis*, 576.
—— —— *rufogularis*, 576.
Ibidorhyncha struthersii, 614.
Ibidorhynchus struthersii, 614.
Ibis leucocephalus, 610.
—— *melanocephalus*, 612.
Ichthyophaga humilis plumbeus, 606.
—— *ichthyaëtus ichthyaëtus*, 606.
Ictinaëtus malayensis, 606.
—— —— *perniger*, 606.
Indicator xanthonotus, 592.
Inocotis papillosus, 612.
Iole icterica, 584.
—— *olivacea cinnamomeoventris*, 584.
—— *virescens*, 584.
Ithagenes cruentus, 622.
Ithagines cruentus, 622.
Ixobrychus cinnamomeus, 610.
—— *minutus minutus*, 610.
—— *sinensis sinensis*, 610.
Ixops nepalensis, 580.
—— *nipalensis*, 580.
Ixulus flavicollis, 580.
—— —— *flavicollis*, 580.
—— *occipitalis*, 580.
—— *striatus*, 580.
Iyngipicus hardwickii, 592.
—— *pygmæus*, 592.
Iynx torquilla, 594.
—— —— *torquilla*, 594.

Jynx torquilla, 594.

Kakatoë moluccensis (Z. S. L.), 1077.
Kallene rufiventris, 570.
Kassina senegalensis, 900.
Ketupa ceylonensis, 602.

Ketupa flavipes, 601.
—— *javanensis*, 602.
—— *ketupa*, 602.
—— *zeylonensis*, 602.
—— —— *hardwickii*, 602.
—— —— *leschenault*, 602.
Kittacincla macroua, 572.
—— —— *indica*, 572.
—— —— *malabarica*, 572.
Kroicephalus ichthyœtus, 616.

Labyrinthodont, 886.
Laiscopus collaris nipalensis, 574.
—— *himalayanus*, 574.
Lalage melaschista avensis, 586.
—— *melaschista melaschista*, 586.
—— *sykesii*, 586.
Lamprocorax panayensis strigatus, 554.
Lanius arenarius, 566.
—— *collurioides*, 564.
—— *cristatus*, 566.
—— —— *cristatus*, 566.
—— —— *isabellinus*, 566.
—— *erythronotus*, 564.
—— *excubitor lahtora*, 564.
—— *hardwickii*, 564.
—— *isabellinus*, 566.
—— *lahtora*, 564.
—— *nigriceps*, 564.
—— —— *nigriceps*, 564.
—— *schach caniceps*, 564.
—— —— *erythronotus*, 564.
—— *tephronotus*, 564.
Larus brunneicephalus, 616.
—— *brunnicephalus*, 616.
—— *ichtyaëtus*, 616.
—— *ridibundus*, 616.
—— —— *ridibundus*, 616.
Larvivora brunnea, 570.
—— *cyana*, 570.
Laticauda colubrina, 1080.
Leiopicus mahrattensis mahrattensis, 592.
Leioptila capistrata capistrata, 580.
—— *melanoleuca melanoleuca*, 580.
Leiothrix luteus, 582.
Lepidosiren paradoxa, 783.
Lepterodius sacer, 610.
Leptocoma asiatica asiatica, 560.
—— *brasiliana*, 560.
—— *flammaxillaris*, 562.
—— *lotenia*, 560.
—— *minima*, 560.
—— *zeylonica*, 560.
Leptomantis indica, 689.
Leptopelis johnstoni, 900.
Leptoptilos argala, 610.
—— *dubius*, 610.
—— *dubus*, 610.
—— *javanica*, 610.
—— *javanicus*, 610.
Lestris pomarinus, 616.
Leucocerca albofrontata, 588.
—— *fuscoventris*, 588.
—— *pectoralis*, 588.
Leucopolius alexandrinus seebohmi, 614.
Limnaetus cristatellus, 604.
—— *kienierii*, 606.
—— *nipalensis*, 604.
—— *niveus*, 604.
Limnesia rugosa, sp. n., 919.
Limonidromus indicus, 560.
Limosa œgocephala, 612.
—— *belgica*, 612.
—— *limosa limosa*, 612.
Lioparus chrysœus, 580.
—— *chrysotis*, 580.
Liopicus mahrattensis, 592.
Lioptila capistrata, 580.
—— *melanoleuca*, 580.
Liothrix luteu, 582.
—— —— *callipyga*, 582.
Lobipluvia malabarica, 614.
Lobivanellus goensis, 614.
—— *indicus indicus*, 614.
Lophactus occipitalis (z. s. l.), 1078.
Lophoceros birostris, 598.
Lophophanes œmodius, 564.
—— *ater œmodius*, 564.
—— *beavani*, 564.
—— *dichrous*, 564.
—— —— *dichrous*, 564.
—— *rubidiventris*, 564.
—— *rufonuchalis beavani*, 564.
Lophophorus impejanus, 622.
—— *impeyanus*, 622.
Lophospizias trivirgatus, 604.
Lophotriorchis kieneri, 606.
Lophura diardi, 624.
—— *rufa*, 622.
Loriculus vernalis, 600.
Loxia curvirostra himalayana, 558.
—— —— *himalayensis*, 558.
—— *himalayana*, 558.
Lymnocryptes minima, 614.
Lyncornis cerviniceps, 598.
—— —— *cerviniceps*, 598.

Macaca, 701.
Machlolphus haplonotus, 564.
—— *jerdoni*, 564.
—— *spilinotus*, 564.
—— *spilonotus*, 564.
—— —— *spilonotus*, 564.
—— —— *subviridis*, 564.
—— *xanthogenys*, 564.
—— —— *aplonotus*, 564.
—— —— *xanthogenys*, 564.
Macropteryx coronata, 596.
Macropygia tusalia, 620.
—— *unchall tusalia*, 620.
Malacocincla abboti abboti, 580.
—— *sepiaria abbotii*, 580.
Malacocircus malabaricus, 578.
—— *malcolmi*, 578.
—— *terricolor*, 578.
Mandrillus, 708.
Mantis inornata, sp. n., 689.
—— *nobilis*, 689.
Mareca penelope, 608.
Marmaronetta angustirostris, 608.
Megalæma marshallorum, 590.
Megalaima caniceps, 590.
—— *lineata*, 590.
—— *virens*, 590.
—— —— *marshallorum*, 590.
—— *viridis*, 590.
Megalixalus brachycnemis, 900.
—— *dorsalis*, 902.
—— *fornasinii*, 900.
Megalornis antigone antigone, 612.
—— *grus lilfordi*, 612.
Megalurus palustris, 566.
Melanocorypha bimaculata, 558.
Melittophagus erythrocephalus erythrocephalus, 598.
—— *swinhoii*, 598.
Melophus melanicterus, 558.
Meniceros bicornis, 598.
Merganser castor, 610.
Mergellus albellus, 610.
Mergus albellus, 610.
—— *castor*, 610.
—— *merganser americanus*, 610.
—— —— *orientalis*, 610.
Merops orientalis birmanus, 598.
—— —— *orientalis*, 598.
—— *philippensis*, 598.
—— *philippinus*, 598.
—— *quinticolor*, 598.
—— *superciliosus javanicus*, 598.
Merops viridis, 598.
Merounga leonina (z. s. l.), 1077.
Merula albocincta, 572.
—— *atrigularis*, 572.
—— *boulboul*, 572.
—— *castanea*, 572.
—— *fuscata*, 572.
—— *obscura*, 572.
—— *ruficollis*, 572.
—— *simillima*, 572.
—— *unicolor*, 572.
Mesia argentauris, 582.
—— —— *argentauris*, 582.
Metopidius indicus, 616.
Microcichla scouleri, 570.
—— —— *scouleri*, 570.
Microhierax cærulescens cærulescens, 606.
—— *eutolmus*, 606.
Micronisus badius, 604.
Microperdix erythrorhynchus, 622.
Micropternus brachyurus, 592.
—— —— *gularis*, 592.
—— —— *humei*, 592.
—— —— *phaiocops*, 592.
—— —— *williamsoni*, 592.
—— *gularis*, 592.
—— *phæocops*, 592.
—— *phaicops*, 592.
Micropus affinis affinis, 596.
—— *melba melba*, 596.
—— *pacificus pacificus*, 596.
—— *phæocephalus*, 584.
Microsarcops cinereus, 614.
Microscelis psaroides ganeesa, 584.
—— —— *psaroides*, 584.
Microtarsus poicephalus, 584.
Miglyptes jugularis, 592.
Milvus govinda, 606.
—— *lineatus lineatus*, 606.
—— *melanotis*, 606.
—— *migrans govinda*, 606.
—— —— *lineatus*, 606.
Minla castaniceps, 580.
—— *cinerea*, 580,
—— *ignotincta*, 582.
Mirafra assamica, 558.
—— —— *assamica*, 558.
—— *cantillans*, 558.
—— —— *cantillans*, 558.
—— *erythroptera*, 558.
Mixornis rubricapilla minor, 580.
—— —— *rubricapilla*, 580.
—— *rubricapillus*, 580,

Molpastes bengalensis, 584.
—— *hæmorrhous*, 584.
—— —— *bengalensis*, 584.
—— —— *hæmorrhous*, 584.
—— —— *nigripileus*, 584.
—— *leucogenys*, 584.
—— —— *leucogenys*, 584.
—— *nigripileus*, 584.
Monticola cinclorhyncha, 574.
—— *erythrogastra*, 574.
—— *solitaria affinis*, 574.
—— —— *pandoo*, 574.
Motacilla alba, 558.
—— —— *alboides*, 558.
—— —— *dukhunensis*, 558.
—— —— *leucopsis*, 558.
—— —— *personata*, 558.
—— *beema*, 560.
—— *borealis*, 560.
—— *cinerea caspica*, 560.
—— *citreola*, 560.
—— —— *calcarata*, 560.
—— —— *citreola*, 560.
—— *citreoloides*, 560.
—— *dukhunensis*, 558.
—— *flava beema*, 558.
—— —— *thunbergi*, 558.
—— *hodgsoni*, 558.
—— *leucopsis*, 558.
—— *lugubris alboides*, 558.
—— —— *leucopsis*, 558.
—— —— *maderas-patensis*, 560.
—— *luzoniensis*, 558.
—— *maderas-patana*, 560.
—— *maderas-patensis*, 560.
—— *melanope*, 558.
—— *personata*, 560.
Mulleripicus pulverulentis, 594.
—— —— *harterti*, 594.
Munia acuticauda, 556.
—— *atricapilla*, 556.
—— —— *atricapilla*, 556.
—— —— *rubronigra*, 556.
—— *malabarica*, 556.
—— *malacca*, 556.
—— —— *orientalis*, 556.
—— *punctulata punctulata*, 556.
—— *rubronigra*, 556.
—— *striata*, 556.
—— —— *acuticauda*, 556.
—— —— *striata*, 556.
—— *undulata*, 556.
Muscadivora ænea sylvatica, 618.
Muscicapula sapphira, 586.
—— *superciliaris*, 586.
Mycerobus carnipes, 556.
—— *melanoxanthos*, 556.
—— *melanoxanthus*, 556.
Mycteria australis, 610.
Myiagra azurea, 588.
Myiomela leucura, 572.
Myiophoneus horsfieldii, 574.
—— *temminckii*, 574.
Myiophonus horsfieldii, 574.
—— *temminckii*, 574.
Mytaras, gen. n., 868.
—— **macrognathus**, sp. n., 868.
Myzornis pyrrhoura, 582.

Nemoricola indica, 560.
Neocuterebra squamosa, 685.
Neophron ginginianus, 602.
—— *percnopterus*, 602.
—— —— *ginginianus*, 602.
Neopus malaiensis, 606.
Neornis flavolivacea, 568.
—— *flavolivaceus*, 568.
—— —— *flavolivaceus*, 568.
Netta rufina, 610.
Nettapus coromandelianus, 608.
Nettion crecca crecca, 610.
Nettium crecca, 610.
Nettopus coromandelianus, 610.
—— —— *coromandelianus*, 610
Niltava grandis, 588.
—— —— *grandis*, 588.
—— *macgrigoriæ*, 588.
—— *sundara*, 588.
—— —— *sundara*, 588.
Ninox scutellatus, 602.
—— *scutulata*, 602.
—— —— *lugubris*, 604.
Nisaetus bonelli, 604.
Nitidula hodgsoni, 586.
Notodela leucura, 572.
Nucifraga caryocatactes hemispila, 552.
—— *hemispila*, 552.
Numenius arquata, 612.
—— —— *lineatus*, 612.
—— *arquatus*, 612.
—— *phæopus*, 614.
—— —— *variegatus*, 614.
Nycticorax griseus, 610.
—— *nycticorax nycticorax*, 610.
Nycticornis athertoni, 598.

Nyroca ferina, 610.
—— —— *ferina*, 610.
—— *ferruginea*, 610.
—— *fuligula*, 610.
—— —— *fuligula*, 610.
—— *nyroca*, 610.
—— —— *nyroca*, 610.
—— *rufa rufa*, 610.

Ochromela nigrirufa, 588.
—— *nigrorufa*, 588.
Œdicnemus crepitans, 612.
—— *scolopax*, 612.
Œnanthe deserti atrogularis, 570.
—— *œnanthe œnanthe*, 570.
—— *opistholeuca*, 570.
—— *picta*, 570.
Œnopopelia tranquebarica, 620.
—— —— *tranquebarica*, 620.
Onychoprion melanauchen, 616.
Ophiderpeton amphiuminus, 874.
Oreicola ferrea, 570.
—— —— *ferrea*, 570.
Oreocincla dauma, 574.
—— —— *dauma*, 574.
—— —— *nilgiriensis*, 574.
—— *mollissima*, 574.
—— —— *mollissima*, 574.
—— *nilgiriensis*, 574.
Oreocorys sylvanus, 560.
Oriolus ceylonensis, 556.
—— *chinensis tenuirostris*, 554.
—— *indicus*, 554.
—— *kundoo*, 554.
—— *melanocephalus*, 554.
—— *tenuirostris*, 554.
—— *traillii*, 556.
—— *xanthornus ceylonensis*, 556.
—— —— *xanthornus*, 554.
Orocetes cinclorhynchus, 574.
—— *erythrogastra*, 574.
Orthosaurus, 886.
Orthotomus longicauda, 566.
—— *sutorius*, 556.
—— —— *patia*, 586.
—— —— *sutorius*, 566.
Ortygornis gularis, 622.
—— *ponticeriana*, 622.
Oryctolagus cuniculus, 755.
Osmotreron affinis, 618.
—— *bicincta*, 618.
—— *malabarica*, 618.
—— *phayrei*, 618.

Otocompsa emeria, 584.
—— *emeria emeria*, 584.
—— —— *fuscicaudata*, 584.
—— —— *peguensis*, 584.
—— *flaviventris*, 584.
—— —— *flaviventris*, 584.
—— *fuscicaudata*, 584.
—— *jocosa*, 584.
—— —— *erythrotis*, 584.
—— *leucogenys*, 584.
Otogyps calvus, 602.
Otothrix hodgsonii, 600.
Otus bakkamœna lettia, 602.
—— —— *plumipes*, 602.
—— *brachyotus*, 600.
—— *sunia sunia*, 602.
—— *vulgaris*, 600.

Pachyglossa melanoxantha, 582.
Palœornis alexandri, 600.
—— *columboides*, 600.
—— *fasciatus*, 600.
—— *javanicus*, 600.
—— *nepalensis*, 600.
—— *rosa*, 600.
—— *schisticeps*, 600.
—— *torquatus*, 600.
Palœospondylus, 783.
Palumbœna eversmanni, 618.
Palumbus casiotis, 620.
—— *elphinstonei*, 620.
—— *pulchricollis*, 620.
Pan, 697.
—— *satyrus* (z. s. l.), 1078.
Pandion haliœtus, 606.
—— —— *haliœtus*, 606.
Papio, 708.
Paradoxornis flavirostris, 582.
Paranaspides lacustris, 791.
Paraphœdon tumidulus, 627.
Parus œmodius, 564.
—— *atriceps*, 564.
—— *cinereus*, 564.
—— *major cinereus*, 564.
—— —— *mahrattarum*, 564.
—— *monticolus*, 564.
Passer cinnamomeus, 556.
—— *domesticus*, 556, 1080.
—— —— *indicus*, 556.
—— *flavicollis*, 556.
—— *indicus*, 556.

Passer montanus, 556.
—— —— *malaccensis*, 556.
—— *rutilans cinnamomeus*, 556.
Pastor roseus, 552.
Pavo muticus, 624.
Pavoncella pugnax, 614.
Pelargopsis amauroptera, 600.
—— *gurial*, 600.
—— *leucocephala*, 600.
Pelecanus javanicus, 608.
—— *onocrotalus roseus*, 608.
—— *philippensis*, 608.
—— *roseus*, 608.
Pelion lyelli, 869.
Pellorneum mandellii, 578.
—— *ruficeps*, 578.
—— —— *mandellii*, 578.
—— —— *subochraceum*, 578.
—— *subochraceum*, 578.
Penthoceryx sonnerati, 594.
—— *sonneratii sonneratii*, 594.
Perdicula argunda, 622.
—— *asiatica*, 622.
—— —— *argoondah*, 622.
—— —— *asiatica*, 622.
—— *erythrorhyncha*, 622.
Perdix hodgsoniæ, 622.
—— —— *hodgsoniæ*, 622.
Pericrocotus brevirostris, 584.
—— —— *brevirostris*, 584.
—— *flammeus*, 584.
—— *peregrinus*, 586.
—— —— *malabaricus*, 586.
—— —— *peregrinus*, 586.
—— —— *vividus*, 586.
—— *roseus*, 586.
—— —— *roseus*, 586.
—— *solaris*, 586.
—— —— *solaris*, 586.
—— *speciosus*, 584.
—— —— *flammeus*, 584.
—— —— *speciosus*, 584.
Perissospiza carnipes, 556.
—— *icteroides affinis*, 556.
Pernis cristata, 606.
—— *cristatus*, 606.
—— —— *ruficollis*, 606.
—— *ptilorhynchus ruficollis*, 606.
Petrocossyphus cyaneus, 574.
Petrophila cinclorhyncha, 574.
—— *cyanus*, 574.
—— *erythrogastra*, 574.
Phalacrocorax carbo, 608.
Phalacrocorax carbo indicus, 608.
—— —— *sinensis*, 608.
—— *javanicus*, 608.
—— *niger*, 608.
Pharyngobolus africanus, 687.
Phasianus wallichii, 624.
Philomachus pugnax, 614.
Phodilus badius saturatus, 600.
Phœnicopterus roseus, 608.
—— *ruber antiquorum*, 608.
Phœnicurus frontalis, 572.
—— —— *frontalis*, 572.
—— *hodgsoni*, 572.
—— *ochrurus rufiventris*, 582.
—— *phœnicurus phœnicurus*, 570.
—— *schisticeps*, 572.
Photodilus badius, 600.
Phragmaticola aëdon, 566.
Phrynobatrachus acridoides, 899.
—— *natalensis*, 899.
Phyllornis aurifrons, 582.
—— *hardwickii*, 582.
—— *jerdoni*, 582.
—— *malabaricus*, 582.
Phylloscopus affinis, 566.
—— *collybitus tristis*, 566.
—— *fuliginiventer*, 566.
—— *fuliginiventris*, 568.
—— *griseolus*, 568.
—— —— *griseolus*, 568.
—— *humei præmium*, 566.
—— *humii præmium*, 566.
—— *indicus*, 568.
—— *lugubris*, 568.
—— *magnirostris*, 568.
—— *proregulus*, 566.
—— —— *newtoni*, 566.
—— *pulcher*, 566.
—— —— *pulcher*, 566.
—— *superciliosus*, 566.
—— *tristis*, 566.
—— *viridanus*, 568.
Pica bottanensis, 552.
—— *pica bottanensis*, 552.
Picumnus innominatus, 594.
—— —— *innominatus*, 594.
Picus barbatus hessei, 590.
—— *brunneifrons*, 592.
—— *canus barbatus*, 590.
—— —— *hessei*, 590.
—— *cathpharius*, 592.
—— *chlorolophus chlorigaster*, 592.
—— —— *chlorolophoides*, 592.

Picus chlorolophus chlorolophus, 590.
—— —— *simlæ*, 592.
—— *macei*, 592.
—— *majoroides*, 592.
—— *mahrattensis*, 592.
—— *squamatus squamatus*, 590.
—— *vittatus dehræ*, 590.
—— —— *myrmecophaneus*, 590.
Piona angulata, 921.
—— **crassipes**, sp. n., 921.
Pipastes agilis, 560.
—— *arboreus*, 560.
—— *montanus*, 560.
Piprisoma agile, 562.
—— *squalidum*, 562.
—— —— *squalidum*, 562.
Pithecus, 699.
Planesticus atrogularis, 572.
—— *fuscatus*, 572.
—— *ruficollis*, 572.
Platalea leucorodia, 612.
—— —— *major*, 612.
Platyrhinops, gen. n., 865.
—— *mordax*, 865.
Plegadis falcinellus, 612.
—— —— *falcinellus*, 612.
Pleuroptyx clavatus, 885.
Ploceus baya, 556.
—— *bengalensis*, 556.
—— *benghalensis*, 556.
—— *manyar*, 556.
—— —— *peguensis*, 556.
—— *megarhynchus*, 556.
—— *passerinus passerinus*, 556.
—— *philippinus*, 556.
—— —— *passerinus*, 556.
Plotus melanogaster, 608.
Pluvialis dominicus fulvus, 614.
Pnoepyga caudata, 576.
—— *pusilla*, 576.
—— —— *pusilla*, 576.
—— *squamata*, 576.
—— —— *squamata*, 576.
Podargus papuensis (z. s. l.), 1078.
Podiceps cristatus, 616.
—— —— *cristatus*, 616.
—— *philippensis*, 616.
—— *ruficollis capensis*, 616.
Podicipes albipennis, 616.
—— *cristatus*, 616.
Polioaëtus humilis, 606.
—— *ichthyaëtus*, 606.
Poliornis teesa, 604.
Polyphasia nigra, 594.
—— *tenuirostris*, 594.
Polyplectron bicalcaratum, 624.
—— *chinquis*, 624.
—— *malaccensis*, 624.
Pomatorhinus albigularis, 578.
—— *erythrogenys*, 578.
—— —— *erythrogenys*, 578.
—— *ferruginosus*, 578.
—— —— *albigularis*, 578.
—— —— *ferruginosus*, 578.
—— *horsfieldii*, 578.
—— —— *travancoriensis*, 578.
—— *hypoleucus*, 578.
—— —— *hypoleucus*, 578.
—— *ruficollis*, 578.
—— —— *ruficollis*, 578.
—— *schisticeps*, 578.
—— —— *schisticeps*, 578.
Pongo, 698.
Porphyrio poliocephalus, 618.
—— —— *poliocephalus*, 618.
Porzana akool, 618.
—— *ceylonica*, 618.
—— *fusca*, 618.
—— *pusilla*, 618.
—— —— *pusilla*, 618.
—— *pygmæa*, 618.
Pratincola atrata, 570.
—— *caprata*, 570.
—— *ferrea*, 570.
—— *indica*, 570.
—— *maura*, 570.
Prinia flavivestris, 568.
—— —— *flavivestris*, 568.
—— *inornata*, 570.
—— —— *burmanica*, 570.
—— —— *inornata*, 570.
—— —— *jerdoni*, 570.
—— *jerdoni*, 570.
—— *socialis*, 568.
—— —— *socialis*, 568.
—— —— *stewarti*, 568.
—— *stewarti*, 568.
—— *sylvatica*, 570.
—— —— *sylvatica*, 568.
Procarduelis nepalensis, 558.
—— *nipalensis nipalensis*, 558.
Proganochelys quenstedtii, 1058.
Proparus chrysæus, 580.
—— *vinipectus*, 580.
Propasser rhodochrous, 558.
—— *rhodopeplus*, 558.

Propasser rodopeplus, 558.
Propyrrhula subhimachala subhimachala, 556.
—— *subhimalayensis*, 556.
Protopterus, 783.
Prunella immaculata, 574.
—— *rubeculoides*, 574.
—— *strophiata*, 574.
Psarisomus dalhousiæ, 590.
Psephoderma alpina, 1058.
Psephophorus polygonus, 1058.
Pseudibis papillosus, 612.
Pseudogyps bengalensis, 602.
Pseudominla castaneiceps castaneiceps, 580.
—— *cinerea*, 580.
Pseudotantalus leucocephalus, 610.
Psittacula alexandri fasciatus, 600.
—— *columboides*, 600.
—— *cyanocephala bengalensis*, 600.
—— *eupatria nepalensis*, 600.
—— —— *nipalensis*, 600.
—— *krameri borealis*, 600.
—— —— *manillensis*, 600.
—— *schisticeps schisticeps*, 600.
Pterocles arenarius, 620.
—— *exustus*, 620.
—— *fasciatus*, 620.
—— *indicus*, 620.
—— *orientalis*, 620.
—— *senegalensis erlangeri*, 620.
Pteroclurus exustus, 620.
Pteruthius æralatus, 582.
—— —— *æralatus*, 582.
—— *erythropterus*, 582.
—— *melanotis*, 582.
—— —— *melanotis*, 582.
—— *ruficenter*, 582.
—— *xanthochloris*, 582.
—— —— *xanthochloris*, 582.
Ptilolæmus tickelli, 598.
—— —— *tickelli*, 598.
Ptyonoprogne rupestris, 588.
Pucrasia macrolopha, 624.
—— —— *macrolopha*, 624.
—— —— *nipalensis*, 624.
Pycnonotus finlaysoni, 584.
—— —— *finlaysoni*, 584.
—— *hæmorrhous*, 584.
—— —— *pygæus*, 584.
—— *plumosus*, 584.
—— —— *plumosus*, 584.
Pycnorhamphus affinis, 556.
—— *carneipes*, 556.
Pyctorhis longirostris, 578.
—— *sinensis*, 578.
—— —— *sinensis*, 578.
Pyrotrogon erythrocephalus erythrocephalus, 596.
—— *fasciatus malabaricus*, 596.
—— *oreskios uniformis*, 596.
Pyrrhocorax pyrrhocorax, 552.
Pyrrhopicus pyrrhotis, 592.
Pyrrhula erythrocephala, 558.
—— *nepalensis*, 558.
—— *nipalensis*, 558.
—— —— *nipalensis*, 558.
Pyrroplectes epauletta, 558.
Pyrrospiza punicea, 558.
—— —— *punicea*, 558.
Pyrrulauda grisea, 558.

Querquedula circia, 610.
—— *crecca*, 610.
—— *querquedale*, 610.

Rallina superciliaris, 618.
—— —— *superciliaris*, 618.
Rallus aquaticus indicus, 618.
—— *indicus*, 618.
Ramphalcyon amauroptera, 600.
—— *capensis burmanica*, 600.
—— —— *gurial*, 600.
Rana adspersa, 897.
—— *angolensis*, 897
—— *ansorgii*, 898.
—— *delalandii*, 897.
—— *galamensis*, 897.
—— *nuttii*, 897.
—— *oxyrynchus*, 898.
Recurvirostra avocetta, 614.
—— —— *avocetta*, 614.
—— *avosetta avosetta*, 614.
Reguloides chloronotus, 566.
—— *erochroa*, 566.
—— *occipitalis*, 568.
—— *proregulus*, 566.
—— *trochiloides*, 568.
—— *viridipennis*, 568.
Rhamphococcyx erythrognathus, 596.
Rheinardia ocellata (Z. S. L.), 846.
Rhipidura albicollis, 588.
—— —— *albicollis*, 588.
—— *albifrontata*, 588.
—— *aureola aureola*, 588.
—— *pectoralis*, 588.

Rhodonessa caryophyllacea, 608.
Rhopodytes tristis, 594.
—— —— *longicaudatus*, 596.
—— —— *tristis*, 594.
—— *viridirostris*, 594.
Rhyacornis fuliginosa, 572.
—— —— *fuliginosa*, 572.
Rhynchaea bengalensis, 614.
Rhyncops albicollis, 616.
Rhyticeros subruficollis, 598.
Rhytidoceros subruficollis, 598.
Rimator malacoptilus, 580.
Riparia paludicola chinensis, 588.
Rodhainomyia chrysidiformis, 685.
Rollulus rouloul, 622.
Rostratula bengalensis, 614.
—— *bengalensis bengalensis*, 614.
—— *capensis*, 614.
Rubigula flaviventris, 584.
Ruticilla cæruleocephala, 572.
—— *frontalis*, 572.
—— *hodgsoni*, 572.
—— *hodgsonii*, 572.
—— *phœnicura*, 570.
—— *rufiventris*, 572.
—— *schisticeps*, 572.
Ruttenia loxodontis, 686.

Sarcidiornis melanotus, 608.
Sarciophorus bilobus, 614.
—— *malabaricus*, 614.
Sarcogrammus indicus, 614.
Sarcogyps calvus, 602.
Sarkidiornis melanotos, 608.
—— *melanotus*, 608.
Saroglossa spiloptera, 554.
—— —— *spiloptera*, 554.
Sasia ochracea, 594.
—— —— *ochracea*, 594.
Sauropatis chloris, 600.
—— —— *chloris*, 600.
Sauropleura marshii, 877.
—— *pectinata*, 877.
Saxicola caprata atrata, 570.
—— —— *bicolor*, 570.
—— *deserti*, 570.
—— *leucuroides*, 570.
—— *œnanthe*, 570.
—— *opistholeuca*, 570.
—— *picata*, 570.
—— *torquata indica*, 570.
Saxicoloides fulicata cambaiensis, 572.
Schlegela wilsoni (Z. S. L.), 1078.
Sciara nitidicollis, 1009.
Sciurus carolinensis, 809.
Scolopax rusticola, 614.
—— —— *rusticola*, 614.
—— *rusticula*, 614.
Scops bakkamœna, 602.
—— *giu*, 602.
Seicercus affinis, 568.
—— *burkii burkii*, 568.
—— *castaneoceps castaneoceps*, 568.
—— *poliogenys*, 568.
—— *xanthoschistos xanthoschistos*, 568.
—— *xanthoschistus albosuperciliaris*, 568.
—— —— *xanthoschistus*, 568.
Serilophus lunatus, 590.
—— —— *lunatus*, 590.
—— *rubrippygius*, 590.
—— *rubropygia*, 590.
—— *rubropygius*, 590.
Sibia capistrata, 580.
—— *picaoides*, 580.
—— —— *picaoides*, 580.
Siphia albicilla, 586.
—— *leucomelanurus*, 586.
—— *parva albicilla*, 586.
—— *strophiata*, 586.
—— —— *strophiata*, 586.
—— *superciliaris*, 586.
Sitta castaneiventris, 562.
—— —— *castaneiventris*, 564.
—— —— *cinnamoventris*, 562.
—— *castaneoventris*, 562.
—— —— *castaneoventris*, 564.
—— *cinnamomeiventris*, 564.
—— *cinnamomeoventris*, 564.
—— *formosa*, 564.
—— *frontalis frontalis*, 564.
—— *himalayensis*, 564.
Sittiparus castaneicepa, 580.
—— *cinereus*, 580.
Siva cyanouroptera cyanouroptera, 580.
—— *cyanuroptera*, 580.
—— *strigula*, 580.
—— —— *strigula*, 580.
Spatula clypeata, 610.
Spelæornis caudatus, 576.
Sphenocercus apicauda, 618.
—— *apicaudus*, 618.
—— —— *apicaudus*, 618.
—— *sphenurus*, 618.
—— —— *sphenurus*, 618.
Spilopelia chinensis suratensis, 620.

Spilornis cheela, 604.
—— —— *albidus*, 604.
—— —— *cheela*, 604.
Spizaëtus cirrhatus, 604.
—— —— *cirrhatus*, 604.
—— —— *limnaëtus*, 604.
—— *limnaëtus*, 604.
—— *nepalensis*, 604.
—— *nipalensis*, 604.
Sporæginthus amandava, 556.
Squatarola helvetica, 614.
—— *squatarola hypomela*, 614.
Stachyridopsis pyrrhops, 580.
—— *ruficeps*, 580.
—— *ruficeps ruficeps*, 580.
Stachyris nigriceps, 580.
—— —— *davisoni*, 580.
—— —— *nigriceps*, 580.
—— *pyrrhops*, 580.
—— *ruficeps*, 580.
Staphidia striata, 580.
—— —— *striata*, 580.
Stegops divaricata, 860.
Stenocypris malcomsoni, 973.
Stercorarius pomarinus pomarinus, 616.
—— *pomatorhinus*, 616.
Sterna albifrons pusilla, 616.
—— *anglica*, 616.
—— *aurantia*, 616.
—— *fuliginosa*, 616.
—— *fuscata infuscata*, 616.
—— *javanica*, 616.
—— *melanauchen*, 616.
—— *melanogaster*, 616.
—— *minuta*, 616.
—— *sumatrana sumatrana*, 616.
Sternula minuta, 616.
Stictospiza formosa, 556.
Stigmatopelia senegalensis cambayensis, 620.
Stoporala albicaudata, 586.
—— *melanops*, 586.
—— —— *melanops*, 586.
Stremmeia scraba, gen. et sp. n., 979.
Streptopelia chinensis suratensis, 620.
—— *decaocto decaocto*, 620.
—— *orientalis ferrago*, 620.
—— *senegalensis cambaiensis*, 620.
Strix candida, 600.
—— *flammea*, 600.
—— *indranee indranee*, 600.
—— —— *newarensis*, 600.
Strix javanica, 600.
—— *nivicola*, 602.
—— *ocellata*, 602.
—— *seloputo*, 602.
Sturnia malabarica, 552.
—— —— *malabarica*, 552.
—— —— *nemoricola*, 552.
—— *malabaricus*, 552.
Sturnopastor capensis capensis, 554.
—— *contra*, 555.
—— —— *contra*, 554.
Sturnus humii, 552.
—— *vulgaris*, 552.
—— —— *humii*, 552.
Surniculus dicruroides, 594
—— *lugubris*, 594.
—— —— *dicruroides*, 594
Sus scrofa (z. s. l.), 1080.
Suthora fulvifrons, 582.
—— —— *fulvifrons*, 582.
—— *nepalensis*, 582.
—— *poliotis*, 582.
—— *ruficeps*, 582.
—— —— *ruficeps*, 582.
—— *unicolor*, 582.
Suya atrigularis, 568.
—— *atrogularis*, 568.
—— —— *atrogularis*, 568.
—— *criniger*, 568.
—— *crinigera*, 568.
—— —— *crinigera*, 568.
—— *fuliginosa*, 568.
Sylochelidon caspius, 616.
Sylvia affinis, 566.
—— *curruca*, 566.
—— —— *affinis*, 566.
Sylviparus modestus, 564.
—— —— *modestus*, 564.
Syncerus caffer (z. s. l.). 1080.
Sypheotides aurita, 612.
—— *auritus*, 612.
Sypheotis aurita, 612.
—— *bengalensis*, 612.
—— *indica*, 612.
Syrnium indranee, 600.
—— *indrani*, 600.
—— *newarense*, 600.
—— *nivicola*, 602.
—— *nivicolum*, 602.
—— *ocellatum*, 602.
—— *seloputo*, 602.
—— *sinense*, 602.

Taccocua leschenaulti, 596.
—— —— *affinis*, 596.
—— —— *sirkee*, 596.
—— *sirkee*, 596.
Tachornis batasiensis. 596.
—— *batassiensis*, 596.
Tachyglossus, 1079.
Tadorna cornuta, 608.
—— *tadorna*, 608.
—— *vulpanser*, 608.
Tantalus leucocephalus, 610.
Tchitrea affinis, 588.
—— *paradisi*, 588.
Temenuchus malabaricus, 552.
—— *pagodarum*, 552.
Tephrodornis pelvica, 556.
—— —— *pelvica*, 556.
—— —— *sylvicola*, 556.
—— *pelvicus*, 556.
—— *pondiceriana pondiceriana*, 556.
—— *pondicerianus*, 556.
Terpsiphone affinis, 588.
—— *paradisi*, 588.
—— —— *affinis*, 588.
—— —— *paradisi*, 588.
Tesia castaneocoronata, 576.
—— —— *castaneocoronata*, 576.
—— *cyaniventer*, 576.
—— —— *cyaniventer*, 576.
—— *cyaniventris*, 576.
Tetraogallus himalayensis, 620.
—— —— *himalayensis*, 620.
Thamnobia cambaiensis, 572.
Tharrhaleus immaculata, 574.
—— *rubeculoides*, 574.
—— *strophiatus*, 574.
Theropithecus, 708.
Threskiornis melanocephalus, 612.
Thringorhina guttata, 580.
—— *striolata guttata*, 580.
Tichodroma muraria, 562.
Tickellia hodgsoni, 568.
Tiga shorei, 592.
Timalia pileata, 578.
—— —— *bengalensis*, 578.
—— —— *jerdoni*, 578.
Timelia pileata, 578.
Timnunculus alaudarius, 606.
—— *cenchris*, 606.
Todirampbus collaris, 600.
Torgos calvus, 602.
Totanus calidris, 612.
—— *fuscus*, 612.
Totanus glareola, 612.
—— *glottis*, 612.
—— *hypoleucus*, 612.
—— *ochropus*, 612.
—— *stagnatalis*, 612.
—— *stagnatilis*, 612.
Toxochelys bauri, 1058.
Tragopan blythi, 622.
—— —— *blythi*, 622.
—— *melanocephalus*, 622.
—— *satyra*, 622.
Treron curvivirostra nipalensis, 618.
—— *nepalensis*, 618.
—— *nipalensis*, 618.
Tribura luteiventris, 566.
—— *luteoventris*, 566.
—— *thoracica*, 566.
—— —— *thoracica*, 566.
Trichostoma abbotti, 580.
Tringa alpina, 614.
—— *cinclus*, 614.
—— *erythropus*, 612.
—— *glareola*, 612.
—— *hypoleucos*, 612.
—— *minuta*, 614.
—— *nebularia*, 612.
—— *ochrophus*, 612.
—— *stagnatilis*, 612.
—— *temminckii*, 614.
—— *totanus totanus*, 612.
Triton vulgaris, 907.
Trochalopteron affine, 576.
—— —— *affine*, 576.
—— *cachinnans*, 578.
—— —— *cachinnans*, 578.
—— *chrysopterum*, 576.
—— *erythrocephalum*, 576.
—— —— *chrysopterum*, 576.
—— —— *erythrocephalum*, 576.
—— *lineatum*, 578.
—— —— *griseicentior*, 578.
—— —— *lineatum*, 578.
—— *phœnicеum*, 576.
—— —— *phœnicеum*, 576.
—— *rufogulare*, 576.
—— *rufogularis*, 576.
—— *squamatum*, 576.
—— *subunicolor*, 576.
—— —— *subunicolor*, 576.
—— *variegatum*, 576.
—— —— *variegatum*, 576.
Troglodytes nipalensis, 574.
—— *troglodytes nipalensis*, 574.

Tropicoperdix chloropus, 622.
Turdinulus brevicaudatus brevicaudatus, 578.
Turdinus abbotti, 580.
Turdoides terricolor malabaricus, 578.
—— —— *terricolor*, 580.
Turdus atrogularis, 572.
—— *boulboul*, 572.
—— *castaneus castaneus*, 572.
—— *eunomus*, 572.
—— *hodgsoni*, 574.
—— *merula albocinctus*, 572.
—— —— *simillimus*, 572.
—— *obscurus obscurus*, 572.
—— *ruficollis*, 572.
—— *unicolor*, 572.
—— *viscivorus*, 574.
—— —— *bonapartei*, 574.
Turnix dussumieri, 620.
—— *maculatus tanki*, 620.
—— *pugnax*, 620.
—— *suscitator taijoor*, 620.
—— *sykesii*, 620.
—— *taijoor*, 620.
—— *tanki*, 620.
Turtur cambayensis, 620.
—— *ferrago*, 620.
—— *humilis*, 620.
—— *meena*, 620.
—— *risorius*, 620.
—— *suratensis*, 620.
Tyto alba javanica, 600.
—— —— *stertens*, 600.
—— *longimembris*, 600.
—— —— *longimembris*, 600.

Upupa epops, 598.
—— —— *epops*, 598.
—— —— *orientalis*, 598.
—— *indica*, 598.
—— *nigripennis*, 598.
Urocichla caudata, 576.
Urocissa flavirostris, 552.
—— —— *flavirostris*, 552.
—— *melanocephala magnirostris*, 552.
—— —— *occipitalis*, 552.
—— *occipitalis*, 552.
—— *sinensis*, 552.
Uroloncha acuticauda, 556.
—— *malabarica*, 556.
—— *punctulata*, 556.
Uroloncha punctulata punctulata, 556.
—— *striata*, 556.
—— —— *acuticauda*, 556.
—— —— *striata*, 556.
Urrua bengalensis, 602.
—— *coromanda*, 602.

Vanellochettusia leucura, 614.
Vanellus cristatus, 614.
—— *vanellus*, 614.
—— *vulgaris*, 614.
Venilia pyrrhotis, 592.
Vivia innominata, 594.
Volvocivora melaschistos, 586.
—— *sykesi*, 586.
Vultur monachus, 602.

Xanthixus flavescens, 584.
—— —— *flavescens*, 584.
Xantholæma hæmacephala indica, 590.
—— —— *luteri*, 590.
—— *hæmatocephala*, 590.
—— *indica*, 590.
Xema brunnicephala, 616.
—— *ridibunda*, 616.
Xenopus lævis, 905.
—— *mulleri*, 905.
Xenorhynchus asiaticus, 610.
—— —— *asiaticus*, 610.
Xiphoramphus superciliaris, 578.

Yuhina gularis, 580.
—— —— *gularis*, 580.
—— *nigrimentum*, 580.
—— —— *nigrimentum*, 580.
—— *occipitalis*, 580.
—— —— *occipitalis*, 580.
Yungipicus hardwickii, 592.
—— —— *hardwickii*, 592.
—— —— *mitchellii*, 592.
—— *pygmæus*, 592.
Yuna torquilla, 594.

Zalophus californianus (E. S. L.), 1077.
Zanclostomus tristis, 594, 596.
—— *viridirostris*, 594.
Zoothera marginata, 574.
—— *monticola*, 574.
Zosterops palpebrosa, 562.
—— —— *palpebrosa*, 562.
—— *palpebrosus*, 562.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

No. 324.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

May 6th, 1930.

Prof. E. W. MacBride, M.A., F.R.S., Vice-President, in the Chair.

The Secretary communicated a note on two Lion-Tiger Hybrids now in the collection of the Munich Zoological Gardens.

Miss E. M. Brown, B.Sc., exhibited, and made remarks upon, some Protozoan Parasites of Fishes.

Mr. E. G. Boulenger, F.Z.S., exhibited (1) living specimens of the Poison-Frog (*Dendrobates tinctorius*), and (2) a male specimen of the Midwife-Toad (*Alytes obstetricans*) carrying the eggs.

Miss S. M. Manton, M.A., Ph.D., F.L.S., C.M.Z.S., communicated her paper "Notes on the Habits and Feeding Mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida).

In the absence of the Author, Dr. S. Zuckerman's paper, on "The Reproduction of the Primates:—I. General Nature and Homology of the Menstrual Cycle," was taken as read.

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W.8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Owing to the lateness of the hour it was agreed, with the Author's consent, to postpone Col. A. E. HAMERTON's Communication "Remarks on Trypanosomiasis in relation to Man and Beast in Africa" until the next Scientific Meeting of the Society.

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 20th, 1930, at **5.30** P.M., when the following Communications will be made:—

Major S. S. FLOWER, O.B.E., F.Z.S.

Exhibition of Photographs of Gorilla, Elephant-Seals, and other animals now in the Carl Hagenbeck Tierpark at Stellingen near Hamburg.

Col. A. E. HAMERTON, C.M.G., D.S.O., F.Z.S.

Remarks on Trypanosomiasis in relation to Man and Beast in Africa.

A. D. MIDDLETON.

The Ecology of the American Grey Squirrel (*Sciurus carolinensis*) in the British Isles.

The following Papers have been received:—

AGNES E. MILLER, M.A.

Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*.

G. CARMICHAEL LOW, M.A., M.D., F.R.C.S., F.Z.S., DOUGLAS DEWAR, B.A., F.Z.S., T H. NEWMAN, F.Z.S., and G. A. LEVETT-YEATS, C.I.E., F.Z.S.

A Classification of the original Watercolour Paintings of Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London.

P. E. P. Deraniyagala, M.A.

Testudinate Evolution.

Margaret C. Steen, B.Sc.

The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio, U.S.A.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary, Zool. Soc.

Zoological Society of London,
Regent's Park, London, N.W. 8

May 13th, 1930.

No. 325.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

May 20th, 1930.

The Lord ROTHSCHILD, D.Sc., Ph.D., F.R.S., Vice-President, in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of April 1930.

Major S. S. FLOWER, O.B.E., F.Z.S., exhibited, and made remarks upon, a series of photographs of Gorilla, Elephant Seals, and other animals now living in the Carl Hagenbeck Tierpark at Stellingen, near Hamburg.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs of the first Pygmy Hippopotamus (*Chœropsis liberiensis*) to be born in the Society's Gardens, the birth having taken place on May 11th.

Col. A. E. HAMERTON, C.M.G., D.S.O., F.Z.S., exhibited a collection of photographs illustrating his "Remarks on Trypanosomiasis in relation to Man and Beast in Africa."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W. 8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. A. D. MIDDLETON communicated his paper on "The Ecology of the American Grey Squirrel (*Sciurus carolinensis*) in the British Isles."

The next Meeting of the Society for Scientific Business will be held on Tuesday, June 3rd, 1930, at 5.30 P.M., when the following Communications will be made:—

G. CARMICHAEL LOW, M.A., M.D., F.R.C.S., F.Z.S., DOUGLAS DEWAR, B.A., F.Z.S., T. H. NEWMAN, F.Z.S., and G. A. LEVETT-YEATS, C.I.E., F.Z.S.

A Classification of the original Watercolour Paintings of Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe in the Library of the Zoological Society of London.

P. E. P. DERANIYAGALA, M.A.

Testudinate Evolution.

MARGARET C. STEEN, B.Sc.

The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio, U.S.A.

A. GIRGIS, M.Sc., M.R.C.S.

The Development of the Heart in the Rabbit.

G. S. SANSOM, M.C., D.Sc., F.Z.S., and J. P. HILL, D.Sc., F.R.S., F.Z.S.

Observations on the Structure and Mode of Implantation of the Blastocyst of *Cavia*.

AGNES E. MILLER, M.A.

Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*.

The following Papers have been received :—

B. J. Marples, B.A.

The Proportions of Birds' Wings and their Changes during Development.

Rachel M. Renton, F.Z.S.

On the Budding of a *Scyphistoma*.

W. H. Thorpe, M.A., Ph.D., C.M.Z.S.

The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* Will. (Diptera Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini).

Baron Francis Nopcsa, C.M.Z.S.

Notes on Stegocephalia and Amphibia.

Peter Gray.

The Attachments of the Urodele Rib to the Vertebra and their Homologies with the Capitulum and Tuberculum of the Amniote Rib.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc

Zoological Society of London,
Regent's Park, London, N.W. 8.
May 27th, 1930.

No. 326.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

June 3rd, 1930.

Sir ARTHUR SMITH WOODWARD, F.R.S., Vice-President, in the Chair.

Mr. J. R. NORMAN, F.Z.S., exhibited, and made remarks upon, the Pectoral Fin of an exceptionally large Flying-Fish (*Exocœtus fernandezianus*) from Juan Fernandez collected by Mr. Arthur Haserick, F.Z.S.

Col. S. MONCKTON COPEMAN, M.D., F.R.S., F.Z.S., exhibited, and made remarks upon, a rare variety of the Waved Umber Moth, *Hemerophila abruptaria* var. *unicolor*, caught on Primrose Hill.

Dr. G. CARMICHAEL LOW, F.Z.S., gave a *résumé* of the "Classification of the original Watercolour Paintings of Birds of India by B. H. Hodgson, S. R. Tickell, and C. F. Sharpe, in the Library of the Zoological Society of London," compiled in collaboration with Messrs. DOUGLAS DEWAR, T. H. NEWMAN, and G. A. LEVETT-YEATS.

Prof. D. M. S. WATSON, F.R.S., F.Z.S., communicated a paper by Mr. P. E. P. DERANIYAGALA, M.A., on "Testudinate Evolution."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W. 8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Miss MARGARET C. STEEN, B.Sc., gave a *résumé* of her paper on "The British Museum Collection of Amphibia from the Middle Coal Measures of Linton, Ohio, U.S.A."

Prof. J. P. HILL, F.R.S., F.Z.S., gave a *résumé* of the two following papers:—(1) "Observations on the Structure and Mode of Implantation of the Blastocyst of *Cavia*," by G. S. SANSOM, M.C., D.Sc., F.Z.S., and J. P. HILL, D.Sc., F.R.S., F.Z.S.; and (2) "The Development of the Heart in the Rabbit," by A. GIRGIS, M.Sc., M.R.C.S.

In the absence of the Author, Miss AGNES E. MILLER'S paper, "Note on the Tail Skeleton of *Lepidosiren paradoxa*, with Remarks on the Affinities of *Palæospondylus*," was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, October 21st, 1930, at 5.30 P.M.

A Notice stating the Agenda for the Meeting will be circulated early in October.

The following Papers have been received:—

B. J. MARPLES, B.A.

The Proportions of Birds' Wings and their Changes during Development.

RACHEL M. RENTON, F.Z.S.

On the Budding of a *Scyphistoma*.

W. H. THORPE, M.A., Ph.D., C.M.Z.S.

The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* Will. (Diptera Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini).

Baron FRANCIS NOPCSA, C.M.Z.S.

Notes on Stegocephalia and Amphibia.

PETER GRAY.

The Attachments of the Urodele Rib to the Vertebra and their Homologies with the Capitulum and Tuberculum of the Amniote Rib.

D. AUBERTIN, M.Sc., A. E. ELLIS, B.A., and G. C. ROBSON, M.A., F.Z.S.

The Natural History and Variation of the Pointed Snail, *Cochlicella acuta*.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
June 10th, 1930.

No. 327.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

October 21st, 1930.

Prof. E. W. MacBride, M.A., F.R.S., Vice-President, in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1930.

Dr. W. T. Calman, F.R.S., F.Z.S., exhibited, and made remarks upon, a photograph of a living *Anaspides tasmaniæ*, on behalf of Miss S. M. Manton, M.A., Ph.D., who was unable to be present at the Meeting.

Prof. T. Thomson Flynn, D.Sc., exhibited, and made remarks upon, a unique collection of Developmental Material from the Echidna (*Tachyglossus*).

Mr. W. H. Thorpe, M.A., Ph.D., C.M.Z.S., communicated his paper on "The Biology, Post-embryonic Development, and Economic Importance of *Cryptochætum iceryæ* Will. (Diptera, Agromyzidæ) parasitic on *Icerya purchasi* (Coccidæ, Monophlebini)."

Sir Arthur Smith Woodward, F.R.S., F.Z.S., gave a *résumé* of Baron Francis Nopcsa's paper, "Notes on Stegocephalia and Amphibia."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W. 8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. PETER GRAY communicated his paper on "The Attachments of the Urodele Rib to the Vertebra and their Homologies with the Capitulum and Tuberculum of the Amniote Rib."

In the absence of the Authors, the following Papers were taken as read:—Dr. C. WALTER, "Report on the Hydracarina: Mr. Omer-Cooper's Investigation of the Abyssinian Freshwaters (Dr. H. Scott's Expedition)"; Miss RACHEL M. RENTON, F.Z.S., "On the Budding of a *Scyphistoma* (Hydrozoa)."

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 4th, 1930, at **5.30** P.M., when the following Communications will be made:—

D. AUBERTIN, M.Sc., A. E. ELLIS, B.A., and G. C. ROBSON, M.A., F.Z.S.

The Natural History and Variation of the Pointed Snail, *Cochlicella acuta*.

W. B. COTTON, I.C.S., F.Z.S.

Exhibition of Ears and Molars of an African Elephant.

THE SECRETARY.

Exhibition of photographs of Elephants taken by Mr. M. A. Wetherall in the Belgian Congo.

J. R. NORMAN, F.Z.S.

Exhibition of photographs of a Living Shark with a Remora attached.

B. J. MARPLES, B.A.

The Proportions of Birds' Wings and their Changes during Development.

A. G. Lowndes, M.A., C.M.Z.S.

On Entomostraca from the New Hebrides collected by Dr. J. R. Baker.

H. W. Parker, M.A.

A Collection of Frogs from Portuguese East Africa.

The following Papers have been received:—

Ieuan Thomas, M.Sc.

The Structure and Life-History of *Sciara nitidicollis* Meig. (Diptera).

Dr. A. Gandolfi Hornyold, F.R.M.S., F.Z.S.

The Otoliths of some large Eels from the Lake of Tunis.

Cyril Crossland, M.A., D.Sc., F.Z.S.

The reduced Building Power and other Variations in the Astrean Corals of Tahiti; with a Note on *Herpetolitha limax* and *Fungia* sp.

W. S. Bristowe, B.A., F.Z.S.

(1) A Contribution to the Knowledge of the Spider Fauna of South-west Ireland, and in particular the Islands off the Coast.

(2) The Spiders of the Island of Grassholm, and some Additions to the Skomer Island List.

S. Maulik, M.A., F.R.M.S., F.E.S., F.Z.S.

On the Larva of the Poisonous Chrysomelid Beetle of N'gamiland, Africa.

A. D. Middleton.

A Contribution to the Biology of the Common Shrew (*Sorex araneus* Linn.).

Herbert Mace, F.E.S.

Dimorphism as a Factor in Evolution.

WILLIAM J. DAKIN, D.Sc., F.Z.S.

The Osmotic Concentration of the Blood of *Callorhynchus millis* and *Epiceratodus forsteri* and the Significance of the Physico-chemical Condition of the Blood in regard to the Systematic Position of the Holocephali and the Dipnoi.

The Rev. E. J. PEARCE, M.A., F.E.S.

Report on the Haliplidæ (Coleoptera): Mr. Omer Cooper's Investigation of the Abyssinian Freshwaters (Hugh Scott Expedition).

H. C. WILKIE, F.R.C.V.S., F.R.M.S., F.Z.S.

The Auditory Organ of the Horse (*Equus caballus*).

MARIE V. LEBOUR, D.Sc., F.Z.S.

(1) Further Notes on Larval Brachyura.

(2) The Larvæ of the Plymouth Caridea.—I. The Larvæ of the Crangonidæ. II. The Larvæ of the Hippolytidæ.

JAMES BROUGH.

On Fossil Fishes from the Karroo System.

A. B. MISRA, D.Sc., F.Z.S.

On the Internal Anatomy of the Female Lac Insect, *Laccifer lacca* Ckll. (Homoptera: Coccidæ).

NELLIE B. EALES, D.Sc., C.M.Z.S.

The Development of the Mandible in the Elephant.

Lt.-Col. J. STEPHENSON, M.B., D.Sc., F.R.S., F.Z.S.

Oligochæta from Burma, Kenya, and other Parts of the World.

R. J. A. W. LEVER.

A New Endoskeletal Organ in the Hind Legs of the Halticinæ (Coleoptera).

M. K. SEREBRENNIKOV.

On the Polychromatism and Albinism of the Siberian Squirrels.

ELLIS LE G. TROUGHTON.

The Occurrence of a Male and Female *Grampus griseus* (Delphinidæ) at Sydney, New South Wales.

Dr. Ernst Schwarz.

A Revision of the Genera and Species of Madagascar Lemuridæ.

J. St. Leger.

A Key to the Families and Genera of African Rodentia.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed, and be limited as far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

Zoological Society of London,
Regent's Park, London, N.W. 8.
October 28th, 1930.

No. 328.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 4th, 1930.

Prof. E. W. McBride, F.R.S., Vice-President, in the Chair.

Mr. G. C. Robson communicated a paper on "The Natural History and Variation of the Pointed Snail, *Cochlicella acuta*," by D. Aubertin, M.Sc., A. E. Ellis, B.A., and G. C. Robson, M.A., F.Z.S.

Mr. W. B. Cotton, I.C.S., F.Z.S., exhibited, and made remarks upon, the Ears and Molars of an African Elephant.

The Secretary exhibited, and made remarks upon, a series of photographs of Elephants taken by Mr. M. A. Wetherall in the Belgian Congo.

Mr. J. R. Norman, F.Z.S., exhibited, and made remarks upon, photographs of a living Shark with a Remora attached.

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W. 8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon :—(1) a red variety of the Common Lobster, and (2) some eggs laid in the Society's Aquarium by a Sea-snake (*Laticauda colubrina*).

Mr. A. G. Lowndes, M.A., C.M.Z.S., gave a *résumé* of his paper, "On Entomostraca from the New Hebrides, collected by Dr. J. R. Baker."

Mr. B. J. Marples, B.A., communicated his paper on "The Proportions of Birds' Wings and their Changes during Development."

Owing to the lateness of the hour, Mr. H. W. Parker's paper on "A Collection of Frogs from Portuguese East Africa" was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 18th, 1930, at 5.30 P.M., when the following Communications will be made :—

The Secretary.

Report on the Additions to the Society's Menagerie during the month of October, 1930.

Prof. R. T. Leiper, F.R.S., F.Z.S.

Exhibition of Helminth Section in the Brain of a Man.

Dr. F. A. Bather, F.R.S., F.Z.S.

Resolutions on Zoological Nomenclature passed at the Zoological Congress at Padua, 1930.

James Brough.

On Fossil Fishes from the Karroo System.

Lt.-Col. J. Stephenson, M.B. D.Sc., F.R.S., F.Z.S.

Oligochæta from Burma, Kenya, and other Parts of the World.

Ieuan Thomas, M.Sc.

The Structure and Life-History of *Sciara nitidicollis* Meig. (Diptera).

Dr. A. Gandolfi Hornyold, F.R.M.S., F.Z.S.

The Otoliths of some large Eels from the Lake of Tunis.

The following Papers have been received :—

Cyril Crossland, M.A., D.Sc., F.Z.S.

The reduced Building Power and other Variations in the Astrean Corals of Tahiti; with a Note on *Herpetolitha limax* and *Fungia* sp.

W. S. Bristowe, B.A., F.Z.S.

(1) A Contribution to the Knowledge of the Spider Fauna of South-West Ireland, and in particular the Islands off the Coast.

(2) The Spiders of the Island of Grassholm, and some Additions to the Skomer Island List.

S. Maulik, M.A., F.R.M.S., F.E.S., F.Z.S.

On the Larva of the Poisonous Chrysomelid Beetle of N'gamiland, Africa.

A. D. Middleton.

A Contribution to the Biology of the Common Shrew (*Sorex araneus* Linn.).

A. B. Misra, D.Sc., F.Z.S.

On the Internal Anatomy of the Female Lac Insect, *Laccifer lacca* Ckll. (Homoptera: Coccidæ).

NELLIE B. EALES, D.Sc., C.M.Z.S.

The Development of the Mandible in the Elephant.

WILLIAM J. DAKIN, D.Sc., F.Z.S.

The Osmotic Concentration of the Blood of *Callorhynchus millis* and *Epiceratodus forsteri* and the Significance of the Physico-chemical Condition of the Blood in regard to the Systematic Position of the Holocephali and the Dipnoi.

The Rev. E. J. PEARCE, M.A., F.E.S.

Report on the Haliplidæ (Coleoptera): Mr. Omer Cooper's Investigation of the Abyssinian Freshwaters (Hugh Scott Expedition).

H. C. WILKIE, F.R.C.V.S., F.R.M.S., F.Z.S.

The Middle Ear of the Horse (*Equus caballus*).

MARIE V. LEBOUR, D.Sc., F.Z.S.

(1) Further Notes on Larval Brachyura.

(2) The Larvæ of the Plymouth Caridea.—I. The Larvæ of the Crangonidæ. II. The Larvæ of the Hippolytidæ.

M. K. SEREBRENNIKOV.

On the Polychromatism and Albinism of the Siberian Squirrels.

ELLIS LE G. TROUGHTON.

The Occurrence of a Male and Female *Grampus griseus* (Delphinidæ) at Sydney, New South Wales.

Dr. ERNST SCHWARZ.

A Revision of the Genera and Species of Madagascar Lemuridæ.

J. ST. LEGER.

A Key to the Families and Genera of African Rodentia.

FRANK COLLINS BAKER, B.Sc., C.M.Z.S.

The Classification of the large Planorboid Snails of Europe and America.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 11th, 1930.

No. 329.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 18th, 1930.

Sir ARTHUR SMITH WOODWARD, LL.D., F.R.S., Vice-President, in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of October, 1930.

THE SECRETARY exhibited, and made remarks upon, a photograph of a House-Sparrow (*Passer domesticus* Linn.), with an abnormal growth of beak.

Prof. R. T. LEIPER, D.Sc., M.D., F.R.S., F.Z.S., exhibited a series of lantern-slides illustrating Helminth infections in the Brain of Man.

Dr. F. A. BATHER, F.R.S., F.Z.S., gave a *résumé* of the Resolutions on Zoological Nomenclature passed at the Zoological Congress at Padua, 1930.

Prof. D. M. S. WATSON, F.R.S., F.Z.S., communicated a paper by Mr. JAMES BROUGH on "Fossil Fishes from the Karroo System."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W. 8, on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Lt.-Col. J. STEPHENSON, M.B., D.Sc., F.R.S., F.Z.S., gave a *résumé* of his paper on "Oligochæta from Burma, Kenya, and other Parts of the World."

In the absence of the Authors the following Papers were taken as read:—IEUAN THOMAS, M.Sc., "The Structure and Life-History of *Sciara nitidicollis* Meig. (Diptera)"; Dr. A. GANDOLFI HORNYOLD, F.R.M.S., F.Z.S., "The Otoliths of some large Eels from the Lake of Tunis."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 3rd, 1930, at 5.30 P.M.

A Notice stating the Agenda for the Meeting will be circulated early in January.

The following Papers have been received:—

CYRIL CROSSLAND, M.A., D.Sc., F.Z.S.

The reduced Building Power and the Variations in the Astrean Corals of Tahiti; with a Note on *Herpetolitha limax* and *Fungia* sp.

W. S. BRISTOWE, B.A., F.Z.S.

(1) A Contribution to the Knowledge of the Spider Fauna of South-West Ireland, and in particular the Islands off the Coast.

(2) The Spiders of the Island of Grassholm, and some Additions to the Skomer Island List.

S. MAULIK, M.A., F.R.M.S., F.E.S., F.Z.S.

On the Larva of the Poisonous Chrysomelid Beetle of N'gamiland, Africa.

A. D. MIDDLETON.

A Contribution to the Biology of the Common Shrew (*Sorex araneus* Linn.).

A. B. Misra, D.Sc., F.Z.S.

On the Internal Anatomy of the Female Lac Insect, *Lacifer lacca* Ckll. (Homoptera: Coccidæ).

Nellie B. Eales, D.Sc., C.M.Z.S.

The Development of the Mandible in the Elephant.

William J. Dakin, D.Sc., F.Z.S.

The Osmotic Concentration of the Blood of *Callorhynchus millii* and *Epiceratodus forsteri* and the Significance of the Physico-chemical Condition of the Blood in regard to the Systematic Position of the Holocephali and the Dipnoi.

The Rev. E. J. Pearce, M.A., F.E.S.

Report on the Halipidæ (Coleoptera): Mr. Omer Cooper's Investigation of the Abyssinian Freshwaters (Hugh Scott Expedition).

H. C. Wilkie, F.R.C.V.S., F.R.M.S., F.Z.S.

The Middle Ear of the Horse (*Equus caballus*).

Marie V. Lebour, D.Sc., F.Z.S.

(1) Further Notes on Larval Brachyura.

(2) The Larvæ of the Plymouth Caridea.—I. The Larvæ of the Crangonidæ. II. The Larvæ of the Hippolytidæ.

M. K. Serebrennikov.

On the Polychromatism and Albinism of the Siberian Squirrels.

Ellis Le G. Troughton.

The Occurrence of a Male and Female *Grampus griseus* (Delphinidæ) at Sydney, New South Wales.

Dr. Ernst Schwarz.

A Revision of the Genera and Species of Madagascar Lemuridæ.

J. St. Leger.

A Key to the Families and Genera of African Rodentia.

FRANK COLLINS BAKER, B.Sc., C.M.Z.S.

The Classification of the large Planorboid Snails of Europe and America.

Major STANLEY S. FLOWER, O.B.E., F.L.S., F.Z.S.

Contributions to our Knowledge of the Duration of Life in Vertebrate Animals.—V. Mammals.

I. FILIPJEV.

Report on Freshwater Nematoda: Mr. Omer-Cooper's Investigation of the Abyssinian Freshwaters (Hugh Scott Expedition).

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 25th, 1930.

I. A. R. I. 75.

IMPERIAL AGRICULTURAL RESEARCH
INSTITUTE LIBRARY
NEW DELHI.

Date of issue.	Date of issue.	Date of issue.
JAN 1955		